

# THE LICHEN FAMILY HEPPIACEAE IN NORTH AMERICA<sup>1</sup>

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## ABSTRACT

This paper is a monographic treatment of the Heppiaceae in continental North America north of Mexico and treats 13 species and 3 varieties. The family occurs mainly in arid areas and is very abundant in parts of the southwestern United States. Culture experiments on the phycobionts and whole lichens are described. Only one lichen substance is reported from the family. This unknown substance occurs in the epithecium and gives a red-violet reaction with KOH and nitric acid. Two genera are recognized—*Heppia*, with one species (*H. lutosa*), and *Peltula* (including *Heterina*). The genus *Heppia* is separated from *Peltula* on the basis of the number of spores per ascus, the gelatinous sheath on the ascus, and the phycobiont.

New combinations made are *Peltula bolanderi* (Ach.) Wetm., *P. clavata* (Kremp.) Wetm., *P. euploca* (Ach.) Wetm., *P. michoacanensis* (B. de Lesd.) Wetm., *P. obscurans* var. *deserticola* (Zahlbr.) Wetm., *P. obscurans* var. *hassei* (Zahlbr.) Wetm., *P. omphaliza* (Nyl. in Eckf.) Wetm., *P. placodizans* (Zahlbr.) Wetm., *P. polyspora* (Tuck.) Wetm., *P. tortuosa* (Nees) Wetm., and *P. zahlbruckneri* (Hasse) Wetm. *Peltula cylindrica* from Georgia is described as new. True *P. tortuosa* is reported from the United States for the first time. Keys, photographs, and maps given for the taxa included along with descriptions and citations of specimens seen.

This paper hopefully begins a series of extensive continental revisions of the lichen family Heppiaceae. The area covered in this study includes all of North America north of Mexico, except Greenland. The Caribbean islands will be included with Mexico in a later paper.

Modern collections are especially necessary for revisions of poorly known families such as this. The Heppiaceae has been somewhat neglected by collectors, because most North American botanists have collected in the summers and few wanted to spend any more time than necessary in the hot deserts. Also, since most of the species are small and easily overlooked, one must actually get down on hands and knees when looking for Heppiaceae. Additional collections were required to give a better idea of total distributions of most of the species, to obtain more adequate material for study, and to observe variation in the field. Three extensive collecting trips were made to find Heppiaceae. The first covered the central and northern Great Plains; the second covered the southern part of the Great Plains west to California; and the third covered the area in between. These three trips covered about 16,500 miles. Over 4,000 lichens were collected, including about 300 of Heppiaceae. All lichen taxa seen at each locality were collected to guard against missing some Heppiaceae and to provide more collections of lichens from arid parts of the United States for other distributional studies.

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In preparing terricolous lichens for the herbarium it is often advisable to glue the soil to prevent crumbling and loss of the specimen. In the Heppiaceae this is an absolute necessity, and even before shipment from the field to the laboratory all terricolous material obtained on these trips was so treated. However, care must be taken so that glue does not soak into the thallus.

#### HISTORY

Of the species now included in the Heppiaceae, the first described was *Lichen euplocus* Ach. in 1798, but this epithet was not brought into the Heppiaceae until 1921. The genus *Heppia* was described by Naegeli *in* Hepp in 1853 with *H. urceolata* Naeg. *in* Hepp as the type species. In 1853 Nylander described the genus *Peltula* with the type species *P. radicata*, but this generic name was not used again until much later.

By 1890 there were numerous species which Wainio (1890) grouped into the tribe Heppieae. In his Brazilian material he recognized one genus, *Heppia*, and divided it into section *Heterina* with two species, section *Pannariella* with two species, and section *Solorinaria* with two species. Zahlbruckner (1907) was the first to recognize the Heppiaceae as a family and included one genus, *Heppia*, with four sections and 40 species. Zahlbruckner (1922–40) lists 94 taxa in the family, and more have been added since.

The first attempt to revise the species of the family was by Hue (1907). He studied and described 23 species and listed 55 more of which he had seen no specimens. Gyelnik (1935) revised the European taxa and described or recognized many small genera within the family. No other revisionary treatment has been attempted, although Harmand (1913) and Hasse (1913) studied the taxa in their areas in some detail.

The first taxon of the family reported from North America was *Heppia despreauxii* reported by Tuckerman *in* Lea (1849) followed by *H. bolanderi* and *H. guepinii* (Tuckerman, 1872). Zahlbruckner described several species, sent to him by Hasse from the western United States, and Bouly de Lesdain described additional taxa from North America, so that today there have been 24 taxa reported from the United States.

Few collectors have collected specimens of Heppiaceae in North America. The outstanding collector was Hasse, who made many collections of the family in southern California, where most of the species occur. These lichens grow in places collectors usually like to skip during summer trips and are small and inconspicuous so they are easily overlooked. It is not surprising that their great abundance has been missed.

#### MORPHOLOGY AND ANATOMY

Most anatomical studies were made on freehand sections. For best results sections of the medulla and cortex should not be over 10–20 $\mu$  thick. Additional sections were made with a freezing microtome for permanent slides. All tissue measurements were made in water, and other measurements were made in KOH.

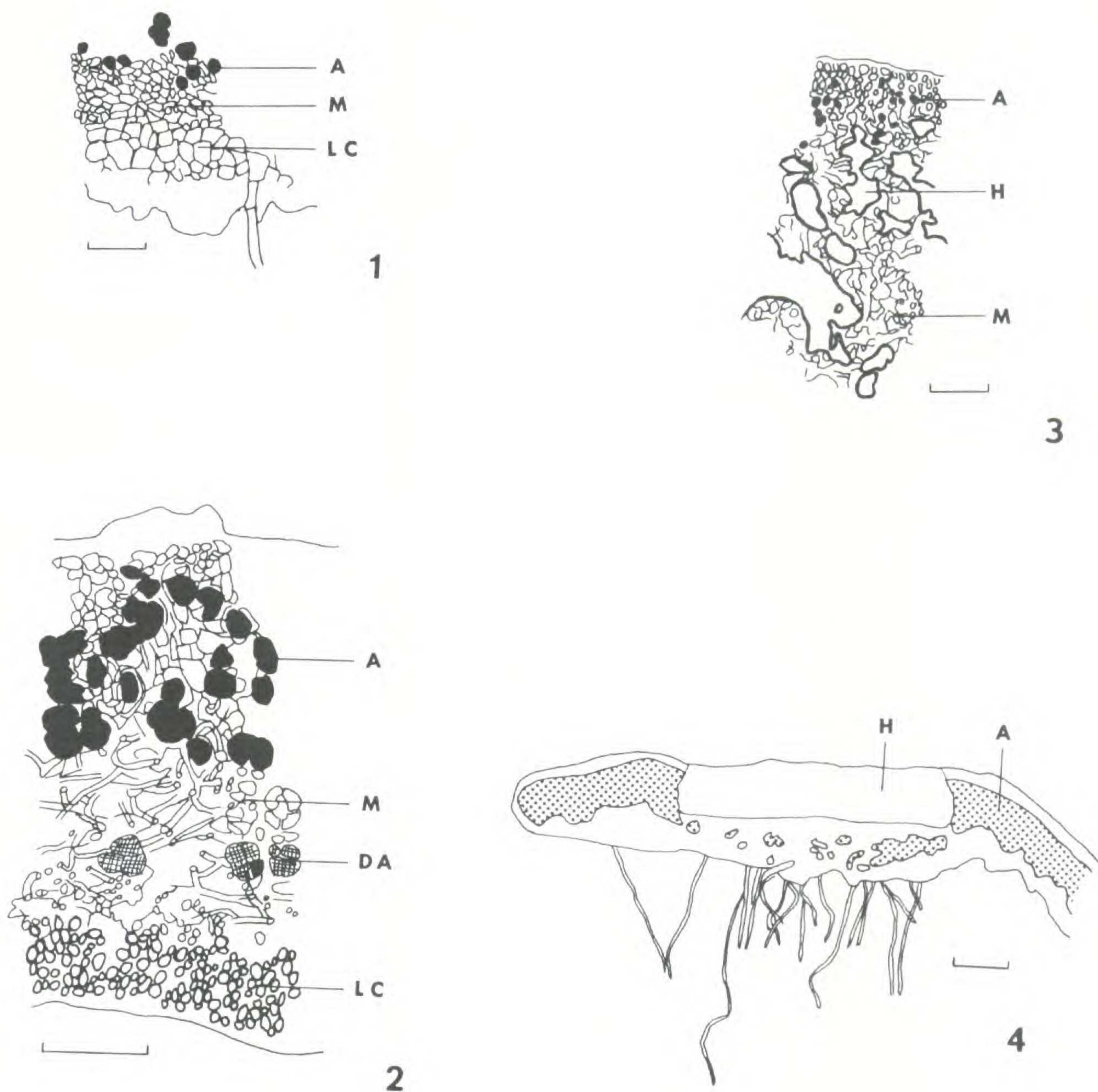
The thallus in the Heppiaceae is mainly squamulose, but in some species it may become areolate or subfruticose. The thallus in *Heppia lutosa* is of flat

squamules which are broadly attached by hyphae. The squamules are more or less roundish and are variable in size from 1–7 mm. In the genus *Peltula* the thallus is areolate, squamulose, peltate, or subfruticose with the thallus units attached at one point. The thallus is more or less roundish and flat to convex and varies from 0.5 mm in diameter in *P. obscurans* var. *deserticola* to 10 mm in diameter in *P. euploca*. In some species the thallus can become deeply lobed and polyphyllous. The attachment is by numerous, large rhizoids or a single umbilicus which may branch at the point of attachment to the substrate. *Peltula placodizans* has an almost areolate thallus in the center but more or less elongated, prostrate, placodiform lobes at the edge. In *Heterina* the thallus is subfruticose and the lobes are terete or flattened and up to 10 mm long and 1 mm thick. The attachment is by a simple umbilicus with one to several lobes attached and ascending from one umbilicus. The umbilicus in *Peltula* may sometimes continue to grow after the main thallus has been broken off. Several times collections of *P. euploca* on rock were seen with additional growth from a naked umbilicus, however, none was seen to redevelop the peltate main thallus.

Soralia are present in three North American species and are either marginal or laminal. In *Peltula bolanderi* the soralia are mainly marginal, while in *P. euploca* the soralia are both marginal and laminal. The soredia are farinose and quite compact in the soralia. In *P. placodizans* soredia are in capitate mounds on the areoles.

Members of the Heppiaceae have a heteromerous thallus with a more or less distinct medulla. A cellular cortex is usually well developed on the lower surface of the thallus and is of the paraplectenchymatous type (Fig. 1). The upper surface rarely has a cortex of any sort but is covered with a thin necral layer. *Heppia lutosa* is paraplectenchymatous throughout, but *Peltula clavata* and *P. richardsii* have no cortices at all. In some cases the lower cortex has cells of different shape or size than the medulla (Fig. 1). But in other cases (*Heppia lutosa*, *Peltula obscurans* var. *obscurans*, and *P. placodizans*) the cells are the same as in the cellular medulla.

The medulla is either paraplectenchymatous or of loose hyphae and can vary from about half of the thallus thickness to almost none. In *Heppia lutosa*, *Peltula polyspora*, and *P. placodizans* there is a continuous paraplectenchymatous medulla (Fig. 1), but in *P. michoacanensis* the medulla is sometimes cellular and sometimes of agglutinate hyphae. To determine the type of medulla very thin sections are necessary. In *Peltula obscurans* the medulla varies from usually cellular in var. *hassei* and var. *obscurans* to usually loose hyphae in var. *deserticola*. The medulla type in *P. obscurans* can vary even within the same thallus lobe from completely cellular to mostly loose with a few cellular areas. In var. *deserticola* and var. *hassei* this seems to be correlated with the pH of the substrate—on calcareous substrates there is less development of cellular tissue in the medulla and lower cortex, but on acid substrates there is better development. A medulla of loose hyphae (Fig. 2) is found in *P. bolanderi*, *P. euploca*, *P. richardsii*, and *P. omphaliza*. In *P. zahlbruckneri* and *P. cylindrica*



FIGURES 1-4. Anatomy of North American Heppiaceae.—1. Lower cortex and cellular medulla of *Peltula polyspora* (Wetmore 17036); A, algal layer; M, medulla; LC, lower cortex. Scale equals  $50\mu$ .—2. Thallus cross section of *Peltula euploca* (Wetmore 14499) showing loose medulla; A, algal layer; M, medulla; DA, dead algae; LC, lower cortex. Scale equals  $50\mu$ .—3. Section of *Peltula cylindrica* (Wetmore 19264) showing hollow areas in medulla; A, algal layer; H, hollow area; M, medulla. Scale equals  $50\mu$ .—4. Section of apothecium of *Heppia lutosa* (Wetmore 13789) showing sunken condition in thallus; H, hymenium; A, algal layer. Scale equals  $100\mu$ .

the medulla is always loose and usually has hollow areas in the center of the thallus lobes (Fig. 3).

The algae always belong to the Cyanophyceae, but in the thallus the colonies are broken up into individual cells or packets of 2-4 cells. In *Heppia* the phycobiont is *Scytonema hoffmannii* Ag. and the cells are single or in packets of two; each cell is  $10-24\mu$  in diameter. In *Peltula* the algae are *Anacystis montana* (Light.) Dr. & Daily and are in packets of 3-4 cells; the cells are  $9-12\mu$  diameter. Both of these determinations were made by Dr. Francis Drouet

from my cultures of the phycobiont. There are many extraneous algae, especially *Nostoc*, associated with the thalli and isolations must be made with care.

Algal cultures were obtained by macerating, then squashing the thallus on a slide, and finally transferring this material to a petri dish of inorganic agar. After about two to four weeks pieces of the thallus were removed from the petri dish to verify which alga was growing out of the thallus. Cultures were repeatedly transferred until uni-algal cultures were obtained.

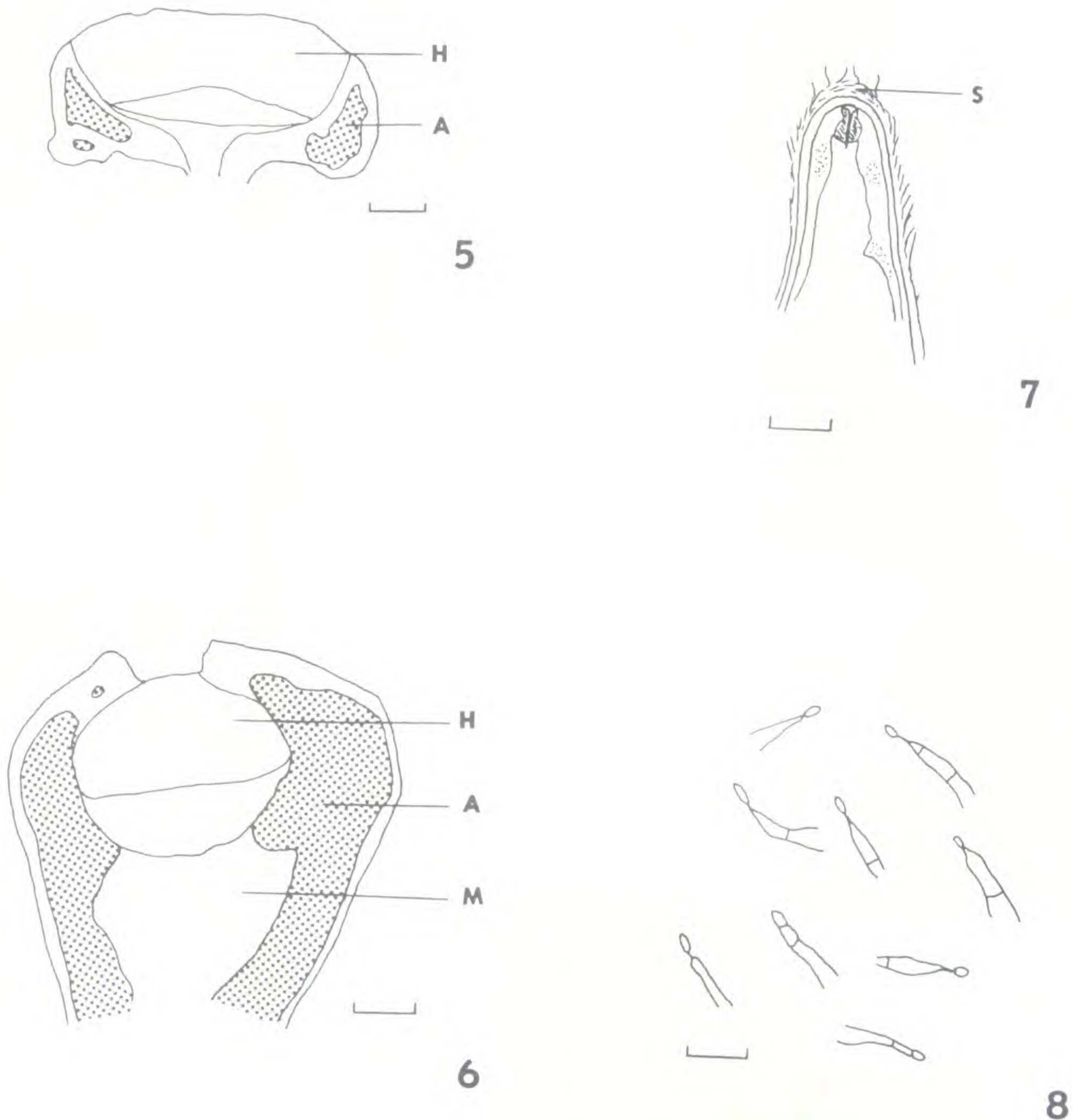
The phycobionts of *Peltula richardsii* and *P. polyspora* were studied in more detail to determine the best culture conditions. These algae were grown in uni-algal cultures under various temperatures from 16°C to 38°C (60°–100°F) and on various inorganic media. The media tried were cyanophycean agar (Starr, 1964), Henriksson's agar (Henriksson, 1964), and Bristol's agar as modified by Bold, including trace elements (Starr, 1964). Petri dishes of media were inoculated with six colonies of cells 0.4 mm in diameter and placed in growth chambers with 200 foot candles of light on 16 hour days. The cultures were allowed to grow for about 4–5 weeks at which time the colonies had grown to a maximum of 1.5 mm diameter.

The optimum culture medium for both phycobionts (both are *Anacystis montana*) was Bristol's agar and the optimum temperature was 27°C (80°F). There were minor differences in growth and appearance between the two phycobionts, but these need further study to determine their significance. The optimum temperature is somewhat higher for the algae tested than the optimum temperature of phycobionts of lichens from more moderate climates (Ahmadjian, 1967). Cyanophycean phycobionts can stand long periods of dryness, and some cultures have been made from herbarium specimens over 20 years old, although no attempt was made to determine the maximum age of collection with revivable algae.

An unsuccessful attempt was made to germinate spores of *Heppia lutosa*, *Peltula obscurans* var. *deserticola* and *P. richardsii*. Soaked apothecia were placed above various agar media and allowed to dry. Apothecia also were placed above agar on which the phycobiont had been growing. A few individual spores were discharged from *Heppia lutosa*, but no spores could be found from the other species, probably partly because of their small size. On two occasions spores of *H. lutosa* produced a germ tube about 20 $\mu$  long at one end of the spore on Bristol's agar, but these failed to develop further. More attempts will be made when abundant fresh material of the lichens is available.

The apothecia of Heppiaceae are immersed to sessile on the upper surface of the thallus. The disc is flush with the upper surface in *Heppia lutosa*, *Peltula michoacanensis*, *P. polyspora*, and *P. richardsii* (Fig. 4). The apothecia in *P. obscurans* are first immersed then sessile or filling the whole squamule (Fig. 5). In *P. bolanderi* it is sessile with a thalloid rim. In *P. euploca*, *P. omphaliza*, *P. placodizans*, *P. zahlbruckneri*, and *P. cylindrica* the apothecia are totally immersed with a punctiform disc (Fig. 6). Apothecia in *P. clavata* are unknown.

The hymenium is 100–200 $\mu$  thick and often pinkish in color. The epithecium of *Peltula polyspora*, *P. obscurans* var. *obscurans*, and *P. richardsii* always has a



FIGURES 5-8. Anatomy and conidiophores of North American Heppiaceae.—5. Section of apothecium of *Peltula obscurans* var. *deserticola* (Wetmore 18294B) showing the apothecium filling the whole squamule; H, hymenium; A, algal layer. Scale equals  $100\mu$ .—6. Section of lobe tip with apothecium of *Peltula cylindrica* (Wetmore 19264) showing immersed apothecium; H, hymenium; A, algal layer; M, medulla. Scale equals  $100\mu$ .—7. Ascus tip of *Peltula polyspora* (Wetmore 14694) showing gelatinous sheath and nature of apical apparatus; S, gelatinous sheath. Scale equals  $10\mu$ .—8. Conidiophores of *Peltula obscurans* var. *hassei* (Wetmore 14539B). Scale equals  $10\mu$ .

fleeting red-violet reaction as KOH or nitric acid is added to the sections on a slide under a microscope. In *P. omphaliza* and *P. placodizans* the reaction is present but is not constant. To detect this reaction it is necessary to watch the

apothecial section as the KOH is added, since the fleeting color only lasts 10–20 seconds and then fades out. Other species lack the  $K^+$  reaction.

The paraphyses are thin ( $1.5\text{--}3\mu$ ) in all species except *Heppia lutosa* where they are usually thicker ( $3\text{--}4.6\mu$ ) and distinctly septate. The paraphyses are unbranched and capitate. The asci are usually  $60\text{--}75 \times 15\text{--}25\mu$  and unitunicate. In species of *Peltula* there is a gelatinous, stringy sheath around the apex (Fig. 7), but in *Heppia lutosa* no sheath is present. The sheath is insoluble in organic solvents and strong acids and bases, but soluble in "Clorox" (a commercial preparation of calcium hypochlorite). The sheath does not stain with iodine, cotton blue, lacto-fuchsin, auto carmine, ferric chloride, or PD. There are eight spores in an ascus in *Heppia lutosa* and up to 100 or more in *Peltula*. The spores are hyaline and nonseptate in all species. Spores are oval-fusiform and large ( $15\text{--}24 \times 6\text{--}10\mu$ ) in *Heppia lutosa*, ellipsoid and small ( $6\text{--}7 \times 3\text{--}4\mu$ ) in *Peltula obscurans*, *P. bolanderi*, *P. michoacanensis*, *P. euploca*, and *P. omphaliza*. Spores are spherical or subspherical and small ( $3\text{--}7\mu$ ) in *Peltula polyspora*, *P. richardsii*, *P. placodizans*, *P. zahlbruckneri*, and *P. cylindrica*. In some older collections of *Heppia lutosa* false septa are present. These false septa are only strands of protoplasm which have also been seen by Henssen in various other genera (Henssen, 1963a, 1963b).

Pycnidia are present but not abundant on the upper surface of the thallus or in the tips of the lobes of the subfruticose thalli. Conidia are exobasidial, fusiform to bacilliform, and  $3\text{--}4 \times 1\text{--}2\mu$  in size (Fig. 8).

#### CHEMISTRY

The Heppiaceae in North America apparently contain none of the usual lichen substances, and none is listed by Culberson (1969). All species available (including numerous exotic species) were screened for substances extractable in hot acetone, benzene, ethyl alcohol, petroleum ether, ethyl ether, chloroform, and methyl alcohol, but no substances could be detected either by examining the residue or by the usual crystallizing reagents. No thallus reactions were detected with KOH or C in the taxa treated here. The only substance found was the pigment in the epithecium of *Peltula polyspora*, *P. richardsii*, and *P. obscurans* var. *obscurans* and occasionally in *P. omphaliza* and *P. placodizans*. This substance is not soluble in any of the above solvents, so no crystals could be detected in the crystallizing reagents. The substance is soluble in KOH and concentrated nitric acid and can be precipitated again by neutralizing the KOH or nitric acid. This substance also occurs in the thallus of some exotic species of Heppiaceae (e.g., *Peltula radicata* Nyl.). It is apparently not the same as any of those in the Caloplacaceae because of its solubility properties. If any of the usual lichen substances are found in the Heppiaceae, they probably will be found in tropical material or in *Heterina*.

The value of the  $K^+$  red-violet substance in the taxonomy of the family is variable. *Peltula polyspora*, *P. richardsii*, and *P. obscurans* var. *obscurans* constantly have the substance and therefore it is useful in identification. In *P. omphaliza* and *P. placodizans* it is not constant, although it is usually present. The main observable difference between *P. obscurans* var. *obscurans* on one hand

and var. *deserticola* and var. *hassei* on the other hand is the  $K^+$  red substance. There is no good correlation of  $K$  reaction and spore shape or lichen habitat, and so I have not recognized them as distinct species.

#### DISTRIBUTION

Species of Heppiaceae occur mainly in the drier parts of the southwestern United States. Only six species occur outside of this area—*Heppia lutos*a, *Peltula euploca*, *P. obscurans* var. *deserticola*, *P. polyspora*, *P. cylindrica*, and *P. zahlbruckneri*.

*Heppia lutos*a has the widest distribution and has been collected in most parts of the United States (Fig. 29). It may be found in the remaining states and should be looked for there. *Peltula euploca* has the next widest distribution (Fig. 31) but is somewhat restricted due to substrate requirements. The greatest number of species occur in California and Arizona.

The predominant distribution type in the Heppiaceae is the Arid Southwestern according to the distribution classification proposed earlier (Wetmore, 1967). *Heppia lutos*a and *Peltula euploca* have Pan Temperate distributions, and *P. polyspora* has a Western Temperate distribution (Fig. 38).

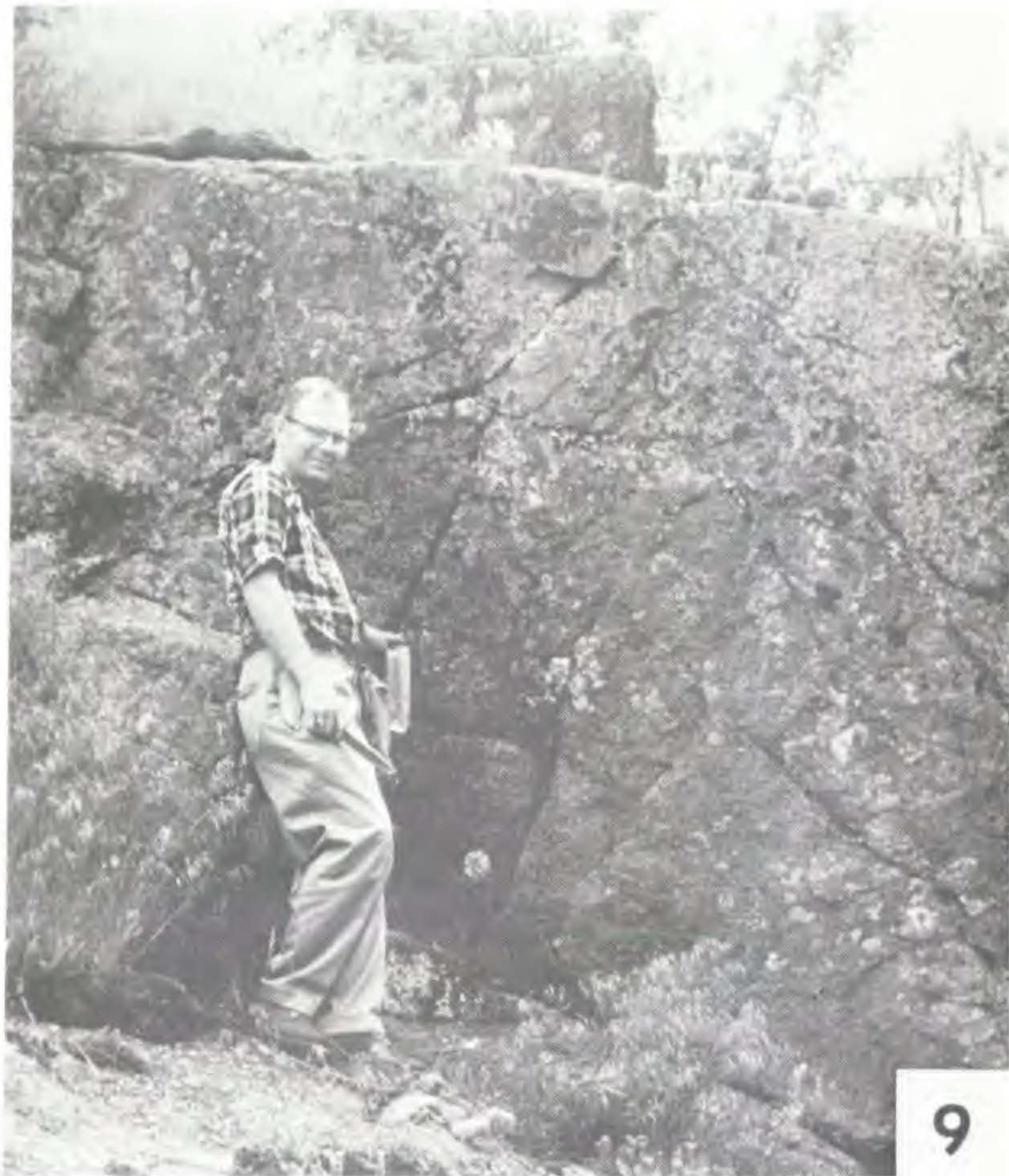
Several species have a very restricted distribution in North America. *Peltula clavata* (Fig. 30) and *P. michoacanensis* (Fig. 32) are only known from one locality north of Mexico. *Peltula zahlbruckneri* has been found only in a few local areas near Los Angeles and Palm Springs, California, and in North Carolina (Fig. 40). Although restricted in areal distribution, *P. zahlbruckneri* is locally abundant. *Peltula cylindrica* has been collected at only five localities around Atlanta, Georgia, in the Georgia Piedmont (Jones, personal communication and Fig. 30), but too little is known of its occurrence to say much about its total distribution in North America. It may be found in other large granitic outcrops in the southern United States.

Many, if not most, of the species found in the United States will probably be found in Mexico, but few collections of Heppiaceae have been made there. Only 24 Mexican localities have come to my attention. These represent 12 taxa, all but four of which are known from areas north of Mexico. Until further collecting is done in Mexico, definitive North American distributions of Heppiaceae cannot be outlined.

Of the 15 taxa occurring north of Mexico, at least six are not known outside of North America: *Peltula bolanderi*, *P. obscurans* var. *deserticola*, *P. placodizans*, *P. richardsii*, *P. zahlbruckneri*, and *P. cylindrica*. However, *P. michoacanensis* may also occur in India, and *P. polyspora* may occur in Europe but identifications of these single collections is not certain. The most widely distributed species in the world is *Heppia lutos*a.

It can be seen that this study represents only a part of the total world distribution of most of the species. Proposed further research to cover Mexico and, eventually, the rest of the world will be necessary to determine more meaningful distribution types.





FIGURES 9-10.—9. Habitat of *Peltula euploca* near Boulder, Colorado. The dark track at the end of the author's hand is *P. euploca* following down a drainage crack in the rock.—10. Habitat of *Peltula cylindrica* on Mt. Arabia, Georgia, looking down-hill. The water drainage runs from bottom center to the rock crack and left. The *Peltula* borders the left side of the drainage track.

## ECOLOGY

Species of Heppiaceae are most abundant in arid and semiarid areas. All species north of Mexico grow on soil or rocks but there is one possible species of Heppiaceae in Mexico which grows on tree bark.

The species usually restricted to rock are *Peltula bolanderi*, *P. clavata*, *P. euploca*, *P. obscurans* var. *deserticola*, *P. omphaliza*, *P. placodizans*, *P. zahlbruckneri*, and *P. cylindricia*. Of these, *P. bolanderi*, *P. clavata*, *P. euploca*, *P. placodizans*, *P. zahlbruckneri*, and *P. cylindricia* are more or less restricted to noncalcareous rocks, and *P. obscurans* var. *deserticola* is usually found on calcareous rocks. *Peltula obscurans* var. *obscurans* and var. *hassei* are often on rock or soil, and *P. omphaliza* occurs on calcareous or noncalcareous rock.

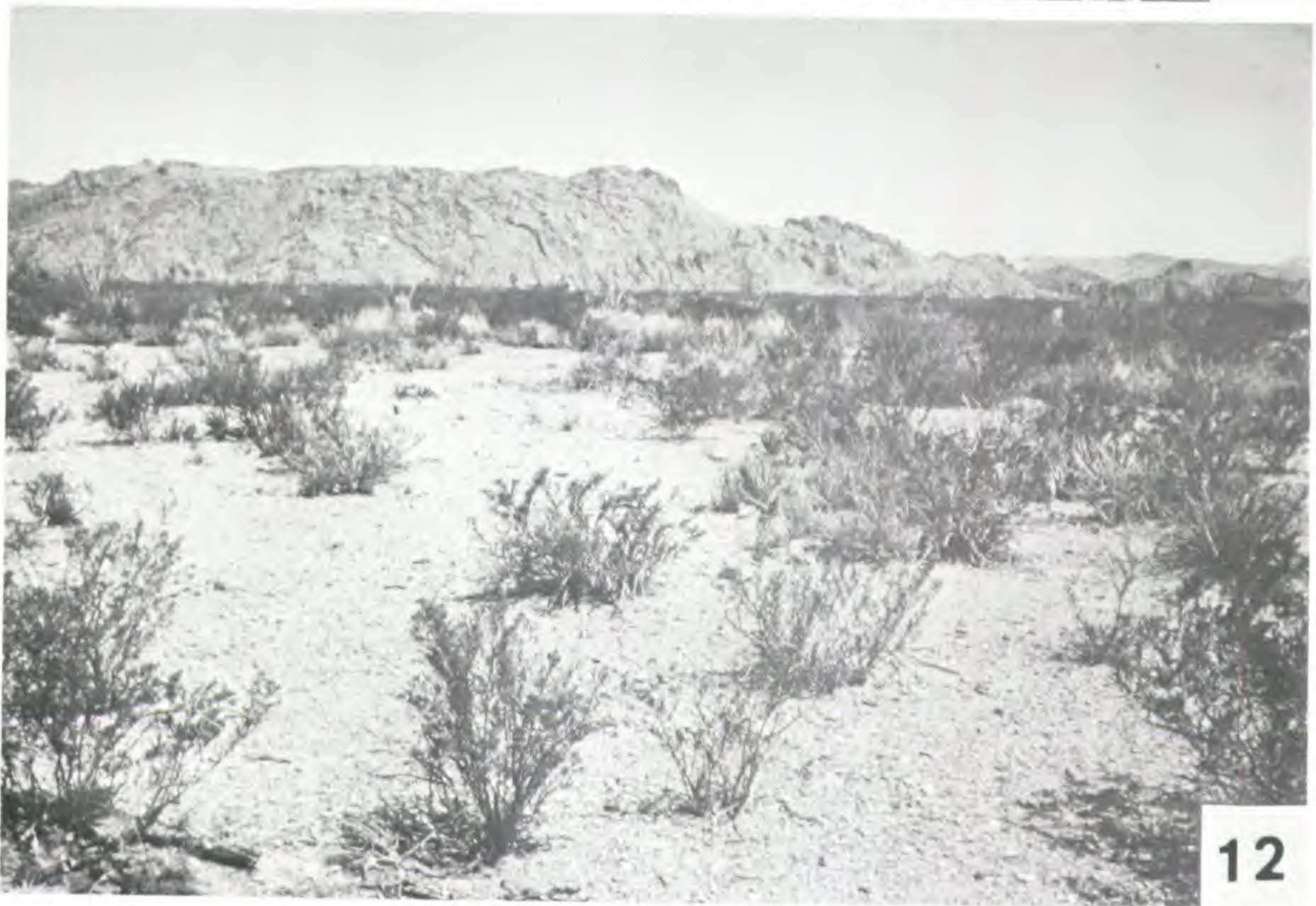
Species usually restricted to soil are *Heppia lutosa*, *P. polyspora*, *P. richardsii*, and *P. michoacanensis*. The soil is usually calcareous.

In all cases a reasonable amount of substrate stability is necessary for growth. No species has been seen on loose, sandy soil, loess, clay, or soft sandstone, probably because of the rapid erosion of the surface. At one locality near Los Angeles, California, *P. euploca* was found on a large conglomerate ledge of rock, but the *Peltula* was only on the hard pebbles and not on the softer matrix. In other localities terricolous species may be found in rock cracks where soil movement is less. Some species occur only on large ledges of rock (Fig. 9). *Peltula euploca*, *P. bolanderi*, *P. zahlbruckneri*, and *P. cylindricia* were only collected on such large expanses of rock and never on small, isolated rocks (Fig. 10). *Peltula cylindrica* grows mainly in water drainage tracks on large granite outcrops (Fig. 10–11). In these tracks it often forms an almost continuous covering. Those thalli growing on higher parts of the granite show poorer growth and are not as abundant. In the eastern part of its range *Heppia lutosa* occurs only on south and southwest facing exposures on banks with sparse vegetation.

*Peltula obscurans* var. *deserticola* grows only on small, calcareous stones. With a little experience, suitable localities could be spotted from the road (Fig. 12). It seems to be restricted to areas with at least 30% of the soil covered with rocks between about 2 and 7 cm in diameter. When it occasionally grows on larger stones, they are not more than about 3 cm above the soil surface. In the optimum habitats with a high density of rocks, it may grow on smaller pebbles too. A possible explanation would be the need for a large enough "target area" for the lichen diaspore to land and become established. On larger stones the lichen grows near the soil surface (it is often found only as a ring near the soil surface) where moisture is greater. Sometimes the stone gets turned over, and another area of thallus will be produced until the whole stone is covered with the lichen.

*Peltula bolanderi* is peculiar in that it is very often found in bubble holes in lava on the underside of large boulders in lava fields (Fig. 13). In large lava beds this species may be abundant on large boulders that are almost too big to roll over. And, therefore, the lichen is very hard to collect, even if it is seen.

*Peltula euploca* grows in two seemingly different habitats. It is found in the mountain areas on the shaded side of rock cliffs associated with intermittent water



FIGURES 11-12.—11. Close view of a drainage track on Mt. Arabia, Georgia. The lighter areas above and below center are *Peltula cylindrica*.—12. Creosote bush desert area near Big Bend National Park, Texas, showing typical habitat of *Peltula obscurans* var. *deserticola*.

seepage (Fig. 9). *Peltula euploca* also grows on the shady side of large, very dry boulders, which probably never have water seepage.

To determine the growth rate of one species, growth rate studies were started on *Heppia lutosa* growing on a roadbank in Iowa in 1965 (Fig. 14), but frost

heaving and other soil movement moved the squamules so that in a one year period no evidence of growth could be seen. When this area was visited again in 1969, almost the whole colony was gone and vascular vegetation had taken over. On checking with the highway department it was found that the roadbank had been graded between 1953 and 1955. Perhaps the lack of evident growth was partly because the colony was on the decline. Some squamules placed in a pot of soil in our garden in Iowa remained the same size and normal in appearance for three years until a tremendous rainstorm covered them with soil. Pieces of thalli of *Heppia lutosa* were placed on sandy soil and loam in the greenhouse. Some were watered from below, while others were watered from above. Within a few weeks salts had accumulated over the thalli to such an extent that they were killed. However, when the pot was covered with glass to retard evaporation, no salts accumulated, and new squamules and apothecia were produced. Pebbles with *Peltula obscurans* var. *deserticola* were placed in a covered glass dish with water in the base. These also produced new squamules after several months. The absence of Heppiaceae on soft rocks also indicates slow growth. This family is very slow to reinvade areas burned by forest fires, and it is useless to look in areas burned less than 30 to 50 years ago for Heppiaceae. In some areas of California these unburned areas are hard to find. But, on the other hand, these lichens are more abundant in drier areas where the vegetation is too sparse to support fires (Fig. 12, 15).

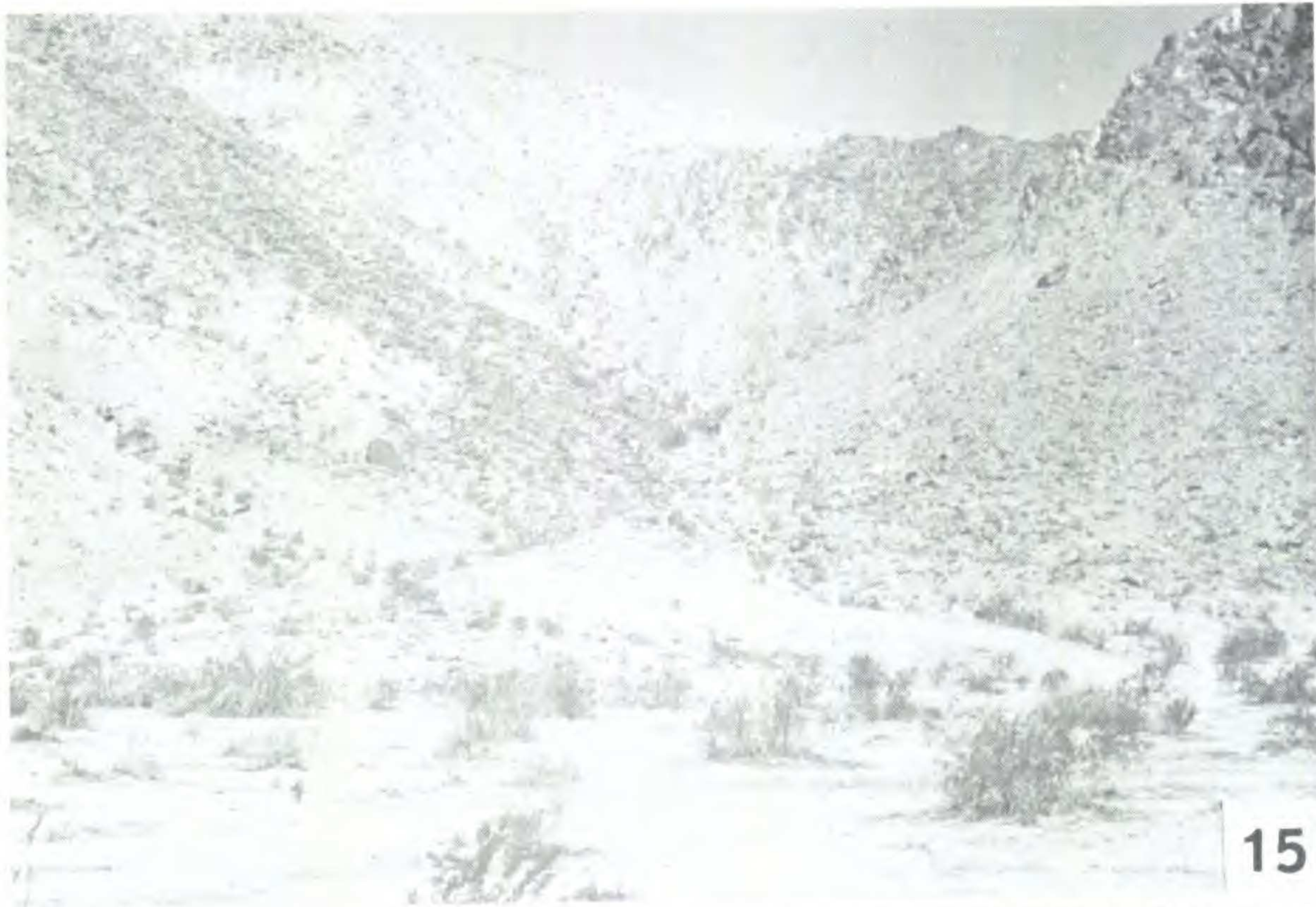
Except in those species with soredia, dispersal in the family is probably largely by thallus fragments. Terricolous species could easily be spread by the numerous, small whirlwinds, or dust devils, which are strong enough to pick up pieces of soil and small pebbles. Spore dispersal could be effective in the dispersal of *Heppia lutosa*, since *Scytonema* is quite common as a free living alga in arid lands. Whether only certain strains of the alga can combine with the fungus is unknown. Soredia are obviously important in the distribution as can be seen by the dense growth of *Peltula euploca* in water tracks over rock ledges (Fig. 9).

Heppiaceae are very abundant in many areas of the southwestern deserts. In many of these areas (Fig. 12, 15) most of the rocks have *Peltula obscurans* var. *deserticola*, and Heppiaceae are the dominant lichens. The growth of some terricolous species is also abundant enough to contribute significantly to soil stabilization, as seen by the extensive hyphal mat around such species as *P. richardsii* and others and the fact that terricolous thalli are usually perched on top of a mound of soil. Since many blue-green algae with heterocysts can fix atmospheric nitrogen (Fay *et al.*, 1968; Granhall & Henriksson, 1969) this family, because of its abundance, may contribute nitrates to an ecosystem which is low in available nitrates by maintaining a population of *Scytonema* in the soil. However, since no heterocysts have been recognized in the thallus, the lichen itself may not contribute to this nitrogen budget. Perhaps the felt of free-living *Scytonema* around the thallus provides nitrates for later growth of the lichen thallus.



FIGURES 13-14.—13. Habitat of *Peltula bolanderi* in central California near Death Valley. The *Peltula* grows in bubble holes on the undersides of these large lava blocks.—14. *Heppia lutosa* habitat near Greene, Iowa, on west-facing roadbank. The area just below the top of the bank had abundant *Heppia* on the bare soil.

The Heppiaceae are well adapted to desert conditions, because of the small squamules which can be easily dispersed by the wind and because of the blue-green algae which can fix nitrogen and withstand long periods of dryness. As a result, this family is slow growing, but so are the other desert plants. The species



FIGURES 15-16.—15. Habitat with Heppiaceae near Palm Desert, California. The rocks on the left side of the valley (north-facing slope) had abundant *Peltula zahlbruckneri*. Other species are abundant on the smaller rocks and soil.—16. *Heppia lutosa* (Wetmore 12579). Scale divisions are 1 mm each.

of the family are not very tolerant to competition from other plants but survive well on barren desert rocks and soil. If the squamules of the terricolous species are displaced by heavy rains, they can continue to grow in new locations, if the soil movement is not too great.

Species of Heppiaceae occur in association with several other lichens that have similar ecological tolerances. *Dermatocarpon hepaticum* (Ach.) T. Fr. usually is found in the same areas. Additional species frequently are *Lecidea decipiens* (Ehrh.) Ach. and *Sarcogyne pruinosa* (Sm. in Sm. & Sowerby) Körb. In some areas other associated species are *Candelariella rosulans* (Müll-Arg.) Zahlbr., *Staurothele clopima* (Wahlenb. in Ach.) T. Fr., *Fulgensia fulgens* (Sw.) Elenk. and species of *Acarospora*, *Toninia*, and other Psoras. Several species of *Acarospora* closely resemble the Heppiaceae in the field but are easily separated by the algae and spores in the lab.

Where Heppiaceae are abundant, several species may be found growing mixed together. Since most Heppiaceae grow as individual squamules, it is easy to find many combinations of *Heppia* and *Peltula* growing on the same piece of substrate.

*Heppia lutosa* has the broadest ecological tolerance and is found from below sea level in Death Valley, California, to above timberline at over 12,200 ft. in Colorado. Most other species occur only at lower elevations and do not reach the alpine tundra.

#### PHYLOGENY

I had planned to delay consideration of the phylogeny and classification of the Heppiaceae until more of the world's species had been studied but brief mention will be made now. These comments and arrangements are tentative and will certainly undergo revision as research on the family continues.

The Heppiaceae has traditionally been placed near the Pannariaceae (Zahlbruckner, 1926), but there is a strong relationship to the Collemataceae also. Both the Collemataceae and the Pannariaceae have filamentous blue-green algae, both have some species with asci with eight spores, some species with septate spores, and some species with heteromerous thalli. The Collemataceae has some species with exobasidial conidia, as does the Heppiaceae, but the Pannariaceae has endobasidial conidia. The medulla in the Collemataceae may be either cellular or loose, while the Pannariaceae has a loose medulla. The Heppiaceae probably belongs between these two families.

Within the Heppiaceae, since several of the exotic genera, such as *Neoheppia*, *Latzelia*, and *Pseudoheppia*, have not been studied, not too much can be said yet. There is a strong possibility that *Gloeoheppia* does not belong in this family. *Heterina* may be a distinct genus, but not enough representatives have been studied to be sure of its disposition. The final arrangement may be close to that of Gyelnik (1935). Based on North American material and a few exotic specimens, *Heppia* is probably the primitive genus followed by the more advanced and more diversified *Peltula* with the subfruticose species the most advanced, at least along the line of thallus development. If genera with septate spores are to be included in the Heppiaceae, they would be on another line of advancement. A cellular medulla is probably primitive in the Heppiaceae, while loose medulla or medulla with hollow areas would be a more advanced condition.

## TAXONOMY

For this study all available collections were borrowed from most of the herbaria in the United States and Canada. Many herbaria had no collections of the family. Citation of herbaria follows Lanjouw and Stafleu (1964). Specimens in several private herbaria were also studied. These are cited as HENSSEN (herbarium of Aino Henssen), KECK (Darvin Keck), SHUSHAN (Sam Shushan), SIERK (Herbert Sierk), THOMSON (John W. Thomson), and WETMORE (Clifford M. Wetmore). If no herbarium is cited for collections, they are in my personal herbarium.

On the distribution maps I have indicated by dots the locality of each collection studied except where many collections occur near each other and the dots would have completely merged. The Mexican collections seen are also mapped, but no attempt was made to borrow all Mexican collections. The collections plotted only give a rough idea of the southern extension of the ranges.

The key and descriptions are based mainly on North American material, but these should be applicable in other areas for all but the rare species. I have some other collections of Heppiaceae from the southwestern United States which I have not been able to place with any of the taxa described here. These are not described as new because they will probably be found more abundantly and better developed in Mexico or other parts of the world. However, *Peltula cylindrica* is described here because it is unlikely that this taxon occurs outside of this study area and because abundant and well developed material was available.

The listing of synonyms under each species is not complete, but includes those names directly pertinent to North America and a few other names where I have seen the types in connection with this study. Under some species numerous additional synonyms will be added as this study is expanded to include other continents.

## KEY TO HEPPIACEAE OF NORTH AMERICA

1. Thallus peltate with finely soresiate margins; on rock . . . . . 2
1. Thallus squamulose, peltate, or subfruticose; without soresiate margins . . . . . 3
  2. Thallus small (1–2 mm diameter), thin (0.2–0.3 mm); margins deeply lobed and undulate; squamules ascending; apothecia sessile with prominent margins; dark olive-green . . . . . *Peltula bolanderi*
  2. Thallus large (3–10 mm diameter), usually thicker (0.2–0.5 mm); margins entire or deeply lobed, downrolled; apothecia usually immersed and disc punctiform; tan to olive . . . . . *Peltula euploca*
3. Thallus placodiform with distinct elongated lobes, areolate in center; with black capitate soralia on the surface; asci polysporous; spores subglobose to globose; on noncalcareous rocks . . . . . *Peltula placodizans*
3. Thallus squamulose, peltate, subfruticose, or areolate but not placodiform; not soresiate . . . . . 4
  4. Apothecia expanded . . . . . 5
  4. Apothecia immersed with punctiform discs or thallus without apparent apothecia . . . . . 13
5. Asci with 8 spores; thallus squamulose; epithecium K<sup>-</sup>; spores 15–24 × 6–10 $\mu$ ; on soil . . . . . *Heppia lutosa*
5. Asci with 16–100 or more spores; spores less than 10 $\mu$  long . . . . . 6
  6. Epithecium K<sup>+</sup> red-violet . . . . . 7
  6. Epithecium K<sup>-</sup> . . . . . 11



7. Thallus black or brown; peltate with many small apothecia or dwarf subfruticose and sterile . . . . . 8
7. Thallus olive; squamulose or areolate . . . . . 9
8. Thallus peltate; many small, immersed apothecia on surface; medulla loose; spores ellipsoid,  $4.6-6.1 \times 3.0\mu$ ; on rock . . . . . *Peltula omphaliza*
8. Thallus dwarf fruticose, finely isidiate; medulla loose with hollow areas; apothecia unknown; on noncalcareous rocks . . . . . *Peltula clavata*
9. Spores globose to subglobose . . . . . 10
9. Spores ellipsoid to oval; medulla cellular; spores  $4.5-7.6 \times 3\mu$  . . . . . *Peltula obscurans* var. *obscurans*
10. Squamules large (2-6 mm diameter), concave; margin entire, downrolled; apothecia large (0.5-3 mm); medulla loose; on soil . . . . . *Peltula richardsii*
10. Squamules smaller (1-4 mm diameter), flat to concave; margin entire when young, slightly lobed when older, usually thickened and upturned; medulla cellular; on soil . . . . . *Peltula polyspora*
11. Thallus deeply lobed, imbricate or polyphyllous, attached by umbilicus; medulla cellular; spores oval,  $6.0-7.6 \times 3.0-4.5\mu$ ; on soil or rock . . . . . *Peltula obscurans* var. *hassei*
11. Thallus only slightly lobed or entire . . . . . 12
12. Squamules deeply concave; apothecia often filling squamules, without raised thalloid rim; medulla cellular; attached by umbilicus; spores  $6.1-7.7 \times 3.4-4.6\mu$ ; on rock with thin layer of soil . . . . . *Peltula michoacanensis*
12. Squamules convex or almost flat; apothecia with raised thalloid rim or filling squamules; medulla usually loose; attached by tuft of rhizoids or umbilicus; on rock . . . . . *Peltula obscurans* var. *deserticola*
13. Growing on rock . . . . . 16
13. Growing on soil . . . . . 14
14. Medulla loose; squamules large (2-6 mm), concave with downturned margins; upper surface of squamules smooth; attached by tuft of few large rhizines . . . . . *Peltula richardsii*
14. Medulla cellular . . . . . 15
15. Broadly attached by rhizoids; often with granular margin; upper surface rough; algae in vertical columns . . . . . *Heppia lutosa*
15. Narrowly attached by umbilicus or few rhizines; margins often deeply lobed . . . . . *Peltula obscurans* var. *hassei*
16. Thallus of scattered isolated, peltate squamules 1-3 mm in diameter; margins slightly lobed; medulla loose; several immersed apothecia per squamule . . . . . *Peltula omphaliza*
16. Thallus not peltate but continuous; squamules deeply lobed or lobes inflated at tips . . . . . 17
17. Thallus lobes flat, thin, deeply lobed; medulla cellular . . . . . *Peltula obscurans* var. *hassei*
17. Thallus lobes swollen and inflated; medulla loose with hollow areas . . . . . 18
18. Thallus close to substrate, not over 1 mm tall; apothecia usually present but immersed . . . . . *Peltula zahlbruckneri*
18. Thallus subfruticose, often to 4-7 mm long, ascending, branched . . . . . 19
19. Lobes terete, not offset, usually one immersed apothecium in the tip of a lobe . . . . . *Peltula cylindrica*
19. Lobes flattened and offset, fertile lobes often larger and with several immersed apothecia per lobe . . . . . *Peltula tortuosa*

## HEPPIACEAE

Heppiaceae Zahlbr. in Engler & Prantl, Nat. Pfl. 1(1\*): 176. 1906.

Tribe Heppiaceae Müll.-Arg., Mém. Soc. Phys. Hist. Nat. Genève 16: 377. 1862.

*Thallus* squamulose to areolate or peltate or subfruticose, heteromerous, paraplectenchymatous throughout or with loose hyphae in the medulla or with hollow areas; apothecia totally immersed or sessile; discs punctiform or open; asci clavate, containing 8-100 or more spores; paraphyses simple and unbranched;

spores hyaline, nonseptate or septate; conidia exobasidial; phycobiont members of Cyanophyceae.

**Heppia** Naeg. *in* Hepp

*Flecht. Eur.* 49. 1853. TYPE: *Heppia urceolata* (Schaer.) Naeg. *in* Hepp [= *Heppia lutosa* (Ach.) Nyl.].

*Thallus* squamulose, broadly attached by hyphae, more or less paraplectenchymatous throughout, usually with a distinct medulla; asci with 8 spores, without gelatinous sheath, spores hyaline, non-septate; phycobiont *Scytonema*.

**Heppia lutosa** (Ach.) Nyl., *Syn. Lich.* 2: 45. 1855.

*Collema lutosum* Ach., *Syn. Lich.* 309. 1814. *Pannaria lutosa* (Ach.) Nyl., *Actes Soc. Linn. Bordeaux* 21: 314. 1856 (= *Prod. Lich. Gall. Alger.*). *Heppia urceolata* var. *lutosa* (Ach.) Boist., *Nouv. Fl. Lich.* 2: 87. 1903. TYPE: Germany, "ad terram limosam." (H, not seen.)

*Solorina despreauxii* Mont. *in* Webb & Berth., *Hist. Nat. Isles Canar.* 3(2): 104. pl. 6, f. 5. 1840. *Heppia despreauxii* (Mont. *in* Webb & Berth.) Tuck., *Gen. Lich.* 46. 1872. *Solorinaria despreauxii* (Mont. *in* Webb & Berth.) Fink, *Lich. Fl. United States* 170. 1935. *Solorina virescens* Mont. *in* Webb & Berth., *Hist. Nat. Isles Canar.* 3(2): 104. 1840. *Heppia virescens* (Mont. *in* Webb & Berth.) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 110. 1857. *Heppia lutosa* \* *H. virescens* (Mont. *in* Webb & Berth.) Nyl., *Syn. Lich.* 2: 45. pl. 9, f. 31. 1885. TYPE: "Ad terram humidam in montibus insulae Canariae," *Despréaux*. (Possible isotype H-NYL.)

*Endocarpon urceolatum* Schaer., *Enum. Crit. Lich. Eur.* 233. 1850. *Heppia urceolata* (Schaer.) Naeg. *in* Hepp, *Flecht. Eur.* 49. 1853. TYPE: "Ad terram in m. Gemmi, Schaer; in Lozère Prost." (Not seen.)

*Lecanora adglutinata* Kremp., *Flora* 34: 675. 1851. *Heppia adglutinata* (Kremp.) Mass., *Geneac. Lich.* 8. 1854. *Pannaria adglutinata* (Kremp.) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 2: 324. 1854. *Heppiomyces adglutinatae* (Kremp.) Cif. & Tom., *Ist. Bot. Reale Univ. Reale Lab. Crittog. Pavia Atti. Ser.* 5.10: 77. 1953. TYPE: "südbaverischen Alpen." (Not seen.)

*Heppia conchiloba* Zahlbr., *Beih. Bot. Centralbl.* 13: 157. 1902. TYPE: California, Palm Springs, in lateribus orientalibus montim San Jacinto, *Hasse FN* 823, 1901. (Holotype W.)

*Heppia macrospora* B. de Lesd., *Ann. Cryptog. Exot.* 5(2): 113. 1932. TYPE: New Mexico, Las Vegas, Kearny's Gap, *Arsène* 20091, 1927. (Lectotype US; isotype FH.)

NOMENCLATORIAL REMARKS. Degelius (1954) studied the type of *Collema lutosum* Ach. and referred it to *Heppia* where it takes priority over the other names which were in use. I have seen photographs of the type material in the Acharian herbarium in Helsinki but was unable to come to any conclusions based on them, and I will accept the findings of Degelius. There is a specimen on the same sheet from France, but since Acharius only mentions material from Germany, that must be considered the holotype.

*Solorina virescens* Mont. *in* Webb & Berth. was used as a synonym under *Solorina despreauxii* in the original description, and so is an obligate synonym based on the same type. Two collections were seen from the Canary Islands (H-NYL 30920 and 30921). These are probably duplicates of the type material.

The holotype of *Heppia macrospora* B. de Lesd. was probably destroyed, and I am selecting the isotype in US as the lectotype.

*Thallus* squamulose (Fig. 16), tan to dark olive; squamules 1–7 mm diameter, concave or flat, roundish to irregular or elongated and folded but not

deeply lobed; margins of larger squamules sometimes granular; upper surface rough and cracked; attached over most of the lower surface by large septate hyphae  $7.6\text{--}12.1\mu$  thick. Thallus  $214\text{--}275\mu$  thick; upper cortex  $30\mu$  thick; lower cortex inseparable from cellular medulla; algal layer  $150\text{--}210\mu$  thick, often filling most of the thallus; algal cells in columns, clumped in pairs of cells or as single cells. *Apothecia* usually one per squamule (rarely up to 10), immersed in upper surface of thallus (Fig. 4); discs expanded,  $0.5\text{--}1.5$  mm, without thalloid rim; epithecium yellowish brown,  $K^-$ ; hymenium  $103\text{--}120\mu$  thick; paraphyses  $3.0\text{--}4.6\mu$  thick, obviously septate with large lumina; asci without gelatinous sheath,  $68 \times 23\mu$ , containing 8 spores; spores hyaline, nonseptate, fusiform,  $15\text{--}24 \times 6.8\text{--}10.3\mu$ . *Hymenium*  $1^+$  wine-red. *Conidia* fusiform  $4.9\text{--}6.1 \times 1.8\text{--}2.4\mu$ .

This species has a Pan-Temperate distribution in North America (Fig. 29). It grows on calcareous soil throughout the United States and north to the Canadian prairie with one collection from the Arctic Slope of Alaska. Common on bare soil and soil banks (Fig. 13).

**TAXONOMIC REMARKS.** A form with large squamules and granular margins was described by Zahlbruckner as *H. conchiloba*, but the granules are not normal soredia. They are produced by a cracking of the margin and are of no taxonomic significance but may serve the same function as soredia in dispersal.

**Exsiccati:** *Plitt, Lich. Exs. 34* (sub *Heppia despreauxii*) (DS, FH, MU), 239 (sub *Heppia terrena*) (ABS, MU).

**STATE UNKNOWN.** Mexican Boundary Survey, mainly in the valley of Rio Grande, *Wright* (FH). Colorado City, *Schantz, 1904* (MICH).

**ALABAMA. COUNTY UNKNOWN:** *Peters, 1874* (FH, MO, US).

**ALASKA.** At Franklin Bluffs on the Sagavanirktok River, *Thomson, Shushan & Koranda 6493* (WIS).

**ARIZONA. COCHISE CO.:** Chiricahua Mts., Cave Creek 6 miles W of Portal, *Weber & Shushan S-8797* (COLO); trail to Silver Peak and Headquarters Gulch, *Weber, Shushan & Anderson, 1960* (COLO, DUKE, PAC, UC). COCONINO CO.: Grand Canyon National Park, South Rim, along Hermit's Rest Trail, *Wetmore 14978*; South Rim, Rowes Well Road near edge of Park, *Wetmore 15019*. MARICOPA CO.: N of Gila Bend near Buckeye on US 80, *Wetmore 14534B*. Saucedo Mts., 14 miles S of Gila Bend along Arizona 85, *Wetmore 14543C*. MOHAVE CO.: In Detrital Valley SW of Hoover Dam on US 93, *Wetmore 14896*. 27 miles E of Kingman near Hackberry along US 66, *Wetmore 14904*. PIMA CO.: Tucson, Station I, *Blumer, 1908* (MICH). Saguaro National Monument NW of Tucson, *Wetmore 14516B*. YUMA CO.: Near Mohawk, E of Yuma on US 80, *Wetmore 14544B, 14547A, 14548A*.

**CALIFORNIA. IMPERIAL CO.:** Near Salton City on west side of Salton Lake, *Wetmore 14551*. INYO CO.: Death Valley National Monument near junction of California 190 and Nevada 58, *Wetmore 14877A*. KERN CO.: E of Maricopa on California 166, *Wetmore 14800A, 14805*. LOS ANGELES CO.: Santa Monica Range, *Hasse* [13 specimens collected between 1897 and 1905] (ABS, DS, FH, LAM, MINN, MU, NY, POM). Newhall, *Farlow, 1897* (FH). Near Soldier's Home, *Hasse, 1897* (UC). San Clemente Island, between Eel Point and Seal Cove, *Weber & Santesson L-43631* (COLO). RIVERSIDE CO.: S of Cathedral City, *Wetmore 16863*. Near western edge of Palm Desert, *Wetmore 16847*. Palm Springs, *Hasse FN 823 p.p.* (W). San Jacinto Mts., west edge of Palm Springs in Chino Canyon, *Wetmore 14625A*. In Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16877*. Near Riverside, Joshua Tree National Monument, *Sipe 1367* (COLO). SAN BERNARDINO CO.: Near Barstow, *Jaeger, 1932* (F). SAN DIEGO CO.: San Diego, *Cleveland, 1875* (US).

**COLORADO. BACA CO.:** SW of Uteville, vicinity of Dodge Ranch, *Shushan S-8156* (COLO). BOULDER CO.: Steamboat Mt., southwest base, 2 miles NW of Lyons, *Weber,*

*Anderson & Awasthi S-17946A* (COLO); southwest slope 1.5 miles NW of Lyons, *Wetmore 16138, 16165, 16183*; south base 1.5 miles N of Lyons, *Weber & Shushan S-17946* (COLO, SHUSHAN); west slope 2 miles NW of Lyons, *Weber L-9901* (COLO). Rocky Mt. National Park, Wild Basin, *Anderson 2122* (COLO). CHAFFEE-GUNNISON COS.: Lake Pass, Sawatch Mts., *Imshaug 11781* (MSC). CONEJOS CO.: 1 mile E of Manassa, *Wetmore 17264*. CUSTER CO.: South Colony Creek, *Kiener 10270* (F). ELBERT CO.: 10 miles NW of Lemon, *Shushan Sl-299* (SHUSHAN). GRAND CO.: Rocky Mt. National Park, 1 mile E of Grand Lake, base of S slope of Mt. Enentah, *Anderson 3467* (COLO, WETMORE); NE of Grand Lake between Summerland Park and Cascade Falls of North Inlet, *Anderson 3254* (COLO). LARIMER CO.: Rocky Mt. National Park, at mouth of Fall River Canyon SE of Endovalley Campground, *Wetmore 15909*; Mummy Range, SE of Lawn Lake, base of Mummy Mt., *Anderson 2064* (COLO); Mummy Range, Mt. Chiquita, *Anderson 2905* (COLO). 22 miles N of Ft. Collins, 2 miles SE of Table Mt., *Anderson S-20233* (ABS, COLO). 19 miles N of La Porte, *Shushan & Weber S-2346* (COLO). Owl Canyon, 9.7 miles N of "Teds Place" (junction of highways 28 and 14), *Shushan & Weber S-4793* (CANL, COLO, FH). 0.5 miles S of Wyoming state line (just N of Virginia Dale), *Shushan Sl-1517* (SHUSHAN). LAS ANIMAS CO.: W of Carrizo Creek, S. of Uteville, *Shushan S-8121* (COLO). LOGAN CO.: 6 miles S of Peetz, *Shushan Sl-319* (SHUSHAN). MESA CO.: N of Colorado National Monument, 3 miles S of Fruita, *Shushan & Weber S-4993* (ABS, CANL, COLO, FH). MONTEZUMA CO.: 22 miles SW of Towaoc, *Shushan & Weber S-680* (COLO). PETKIN CO.: Elk Mts., trail from Conundrum Pass to Conundrum Hot Springs Guard Station, *Weber & Shushan S-5980* (COLO). SUMMIT CO.: Loveland Pass, *Wetmore 16332*. WELD CO.: Eastern end of Chalk Bluffs, 3 miles S of Wyoming state line (Cox Ranch), *Shushan S-2533* (COLO, DUKE, LAM, WIS). 0.5 mile SW of Twin Pawnee Buttes, *Shushan & Higgins S-4900* (COLO, US, WTU). YUMA CO.: 6 miles E of Wray, *Shushan & Anderson L-32966* (COLO). Wray, high plains, *Kiener 6362* (F, WTU). South edge of Wray, *Wetmore 15742*.

FLORIDA. COUNTY UNKNOWN: *Calkins s.n.* (MICH). OSCEOLA CO.: Ashton, *Moore 6244* (WETMORE). POLK CO.: 7 miles E of Avon Park, *Wetmore 13789*. SEMINOLE CO.: Markham, *Rapp, 1929* (YU). Sanford, *Rapp, 1912* (FH, US). VOLUSIA CO.: Daytona, *Thaxter 243* (FH, MICH).

GEORGIA. MCINTOSH CO.: Darien, *Ravenel, 1882* (PH).

ILLINOIS. COUNTY UNKNOWN: *Calkins s.n.* (F), *Hall, 1879* (FH, US). FULTON CO.: Canton, *Miller 72* (BKL), *Wolf* (PH, US). MENARD CO.: Athens, *Hall, 1862* (F, FH, WIS). MONROE CO.: Fults, *Skorepa 1853* (WETMORE).

IOWA. BUTLER CO.: 3 miles S of Greene along Iowa 14, *Wetmore 12579*. CLAYTON CO.: Pikes Peak, bluffs along Mississippi River near McGregor, *Imshaug 27883* (MSC). FAYETTE CO.: *Fink, 1894* (ABS, CANL, CINC, CUP, F, FH, MICH, MINN, MO, MU, NY, OS, POM, US, WIS, THOMSON). 2.5 miles W of Fayette on highway 93, *Niemann 33* (WETMORE). WINNESHIEK CO.: E of Decorah, *Wetmore 15451*.

KANSAS. FRANKLIN CO.: 1 mile SW of Ottawa, *Kramer 483* (WIS). LEAVENWORTH CO.: 4 miles NE of Tonganoxie, *McGregor 1428* (MO). LOGAN CO.: 4 miles SW of Eldadeer, *McGregor 2151* (MO).

MASSACHUSETTS. MIDDLESEX CO.: Cambridge, opposite Mt. Auburn gate, *Tuckerman, 1853* (FH).

MINNESOTA. BROWN CO.: New Ulm, *Fink 284* (MINN). BLUE EARTH CO.: Mankato, *Fink 177* (MINN). KANDIYOHI CO.: Locality unknown, *Looman, 1961* (WIS). OTTER TAIL CO.: Battle Lake, *Fink 57* (MINN). Leaf Hills, *Fink 232* (MICH, MINN, US). PENNINGTON CO.: Thief River Falls, *Fink 773* (MINN). YELLOW MEDICINE CO.: Granite Falls, *Fink 507* (MINN).

MISSOURI. FRANKLIN CO.: Missouri Botanical Garden Aboretum, Gray Summit, *Anderson, 1949* (CUP). JEFFERSON CO.: Crystal City, *Russell 142* (MICH, MO). PERRY CO.: Perryville, *Demetrio 13* (NY, PH).

MONTANA. CUSTER CO.: 10 miles SW of Miles City along US 10, *Wetmore 12840, 12846*. DAWSON CO.: 10 miles SW of Glendive, *Wetmore 12783, 12786, 12790B, 12793, 12807*. ROOSEVELT CO.: Locality unknown, *Looman, 1961* (CANL, WIS). ROSEBUD CO.: W of Forsyth above campground, *Wetmore 12870*.

NEBRASKA. CASS CO.: 4 miles SE of Elmwood, *Kiener 13637* (COLO). CHERRY CO.: In city park in Valentine, *Wetmore 13094A*. CUSTER CO.: 2 miles E of US 183 on Nebraska 92 (21 miles W of Loup City), *Wetmore 13112, 13113*. DODGE CO.: Fremont, *Kiener 24413*

(WETMORE). HARLAN CO.: Along US 6, 8 miles S of Atlantic, *Wetmore 15714*. LANCASTER CO.: 7 miles NW of Lincoln, *Kiener 9704* (F, FH, WTU). POLK CO.: 4 miles E of Platte River along Nebraska 92, *Wetmore 13118*. SARPY CO.: S of Melia, *Kiener 8274* (F).

NEVADA. CLARK CO.: Along US 91 NE of Las Vegas 22 miles at road to Axial, *Wetmore 17035B, 17039*. Near Gold Butte, *Tavares 31d* (UC). NYE CO.: Near Mercury along US 95, *Wetmore 14894A*.

NEW MEXICO. LINCOLN CO.: Carrizozo, Tularosa Basin Las Vegas, *Shields 21, Shields 7, Shields 6a* (all WTU). MCKINLEY CO.: Cibola National Forest at Quaking Aspen Campground, SE of Gallup, *Wetmore 15132, 15134*. Along US 66 at road to Manvelito 13 miles W of Gallup, *Wetmore 15076*. OTERO CO.: Lincoln National Forest, 2 miles E of Mountain Lake (E of Alamogordo), *Wetmore 14412*. SAN JUAN CO.: 7 miles E of Blanco, *Shushan S-7906* (ABS, COLO, MSC). SAN MIGUEL CO.: Las Vegas, Kearny's Gap, *Arsène 20091* (FH, US), Agua Zarca, *Arsène 19698* (FH, US). Kearny's Gap, W of Las Vegas on road to Mineral Hill, *Wetmore 15159, 15161*. 3 miles E of Las Vegas on New Mexico 65, *Wetmore 15144*. TAOS CO.: 4 miles S of Tres Piedras, *Shushan & Weber S-6547* (COLO). UNION CO.: Capulin Mt. National Monument, *Wetmore 15200*. 3 miles N of Capulin Mt. National Monument, *Wetmore 17421, 17468, 17472*. 7 miles E of Folsom, *Shushan S-11407* (COLO). VALENCIA CO.: Along San Jose River, 3.5 miles SE of Correo on road to Las Lunas, *Shushan & Weber S-6890* (COLO).

NEW YORK. ROCKLAND CO.: Tomkins Cove, *Fleming, Fleming & Nearing, 1963* (COLO, NY, NYS). WARREN CO.: Glen's Falls, *Willey, 1872* (US).

NORTH CAROLINA. COUNTY UNKNOWN: *Curtis* (FH).

NORTH DAKOTA. BILLINGS CO.: S of Medora in North Dakota Badlands, *Wetmore 12768*. NORTON CO.: 4 miles W of Mandon along US 10, *Wetmore 12709*.

OHIO. HAMILTON CO.: Cincinnati, *Lea, 1843* (FH, PH, US).

OKLAHOMA. MARSHALL CO.: Near Happy Hollow, *Keck 1773* (KECK). MURRAY CO.: Platt National Park, *Wetmore 14120*. TEXAS CO.: 7 miles NE of Guyman on US 54, *Wetmore 15227*.

SOUTH CAROLINA. COUNTY UNKNOWN: Locality unknown, *Tuckerman* (BLK), *Curtis* (NYS). AIKEN CO.: Santee District, Aiken, *Ravenel 465* (FH). DARLINGTON CO.: Society Hills, *Curtis, 1850* (FH, NY).

SOUTH DAKOTA. CUSTER CO.: 3.6 miles S of US 16 on Fourmile Creek Road (4 miles W of Custer), *Wetmore 6705* (MSC). LAWRENCE CO.: Spearfish Canyon S of Bridal Veil Falls (6 miles S of Spearfish), *Wetmore 11107* (MSC). 5 miles NW of Spearfish, *Wetmore 11191* (MSC). PENNINGTON CO.: 3 miles WSW of Rapid City, E of Dark Canyon, *Anderson S-20580* (COLO, MSC). Matt Burn, 2 miles SE of Deerfield Reservoir, *Wetmore 12524*. E of Hayward (15 miles SSW of Rapid City), *Wetmore 11058* (MSC, WETMORE), *Wetmore 11038, Wetmore 11044* (both MSC).

TENNESSEE. ANDERSON CO.: Savage's Garden, *Sharp, 1957* (WIS). HAMILTON CO.: Chattanooga, *Calkins, 1892* (PH). Mission Ridge, *Calkins s.n.* (CUP, F, FH, MICH, MINN, MO, NY, PAC, THOMSON).

TEXAS. COUNTY UNKNOWN: Locality unknown, *Wright, 1852* (FH); Mexican Boundary Survey, in valley of Rio Grande below Doñana, Hills of the Blanco, *Wright, 1850* (FH); Organ Mts., *Wright 58, 32* (FH). BREWSTER CO.: Big Bend National Park, along Lost Mine Trail from Panther Pass, *Wetmore 14265B*; 2 miles W of junction with road to Castolon, *Wetmore 18303*; Dagger Flats, *Wetmore 18205, 18215*; Hot Springs near Rio Grande Village, *Wetmore 18189, 18193*; Old Mine Road near Rio Grande Village, *Wetmore 18377, 18381*; Pulliam Ridge, *Wetmore 18203A*. BROWN CO.: SW of Brownwood on US 67, *Wetmore 14209, 14211*. CAMERON CO.: NE of Resaca Park, Brownsville, *Runyon 3819a* (MO). JOHNSON CO.: Cleburne State Park (SW of Cleburne), *Wetmore 14163, 14190*. REEVES CO.: N of Pecos along US 285, *Wetmore 14313, 14317B*. UPTON CO.: N of McCamey in King Mt. area, *Wetmore 14243*.

UTAH. EMERY CO.: San Rafael River, Buckhorn Wash, *Flowers 892* (COLO). GRAND CO.: Delores River, 1 mile E of junction with Colorado River, *Flowers 1057* (COLO). KANE CO.: Colorado River at Rock Creek, *Flowers 807* (COLO, DUKE). UINTAH CO.: Dinosaur National Monument, mouth of Split Mountain Gorge, *Anderson, Awasthi & Dahl S-29387* (COLO, DUKE). WASHINGTON CO.: 13 miles W of Santa Clara along US 91, W of St. George in Shivwits Indian Reservation, *Wetmore 17056*.

VERMONT. RUTLAND CO.: Wallingford, *Schallert 18168* (F).

WISCONSIN. DANE CO.: Madison, collector unknown (WIS). IOWA CO.: Mill Creek, 6 miles W of Arena, *Wetmore* 13175, 13217.

WYOMING. CARBON CO.: Snowy Pass, Medicine Bow National Forest, 43 miles E of Laramie, *Shushan* S-9830 (COLO).

SASKATCHEWAN. ASSINIBOIA CO.: Locality unknown, *Looman*, 1961 (WIS, CANL).

Specimens also seen from Mexico, Bermuda, Canary Islands, and Europe.

### ***Peltula* Nyl.**

Ann. Sci. Nat. Bot. Sér. 3. 20: 316. 1853 and Mém. Soc. Sci. Nat. Cherbourg 2: 322. 1853. *Heppia* sect. *Peltula* (Nyl.) Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 215. 1890 (= Étude Lich. Brésil 1: 215, footnote. 1890). TYPE: *Peltula radicata* Nyl.

*Endocarpiscum* Nyl., Flora 47: 487, footnote. 1864. TYPE: *Endocarpiscum guepinii* (Del. in Duby) Nyl. [= *Peltula euploca* (Ach.) Wetm.].

*Guepinia* Hepp, Verh. Schweiz. Naturf. Ges. 48: 85. 1864. TYPE: *Guepinia polyspora* Hepp [= *Peltula euploca* (Ach.) Wetm.].

*Guepinella* Bagl., Nuovo Giorn. Bot. Ital. 2: 174. 1870. TYPE: *Guepinella myriocarpa* Bagl. [= *Peltula euploca* (Ach.) Wetm.].

*Heppia* sect. *Pannariella* Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 215. 1890 (= Étude Lich. Brésil 1: 215. 1890). *Pannariella* (Wain.) Gyel., Repert. Spec. Nov. Regni Veg. 38:307. 1935. TYPE: *Pannariella bolanderi* (Tuck.) Gyel. [= *Peltula bolanderi* (Tuck.) Wetm.].

*Heppia* sect. *Placoheppia* Zahlbr., Bull. Torrey Bot. Cl. 35: 300. 1908. *Solorinaria* sect. *Placoheppia* (Zahlbr.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 307. 1935. *Placoheppia* (Zahlbr.) Oksn., Fl. Lich. Ucrain. 1: 407. 1956 (*comb. inval.*). TYPE: *Heppia placodizans* Zahlbr.

*Thallus* areolate, squamulose, peltate or subfruticose, attached by small area of rhizines or umbilicus; paraplectenchymatous throughout or with loose medulla; asci with 16–100 or more spores, with gelatinous sheath; spores hyaline, non-septate; phycobiont *Anacystis*.

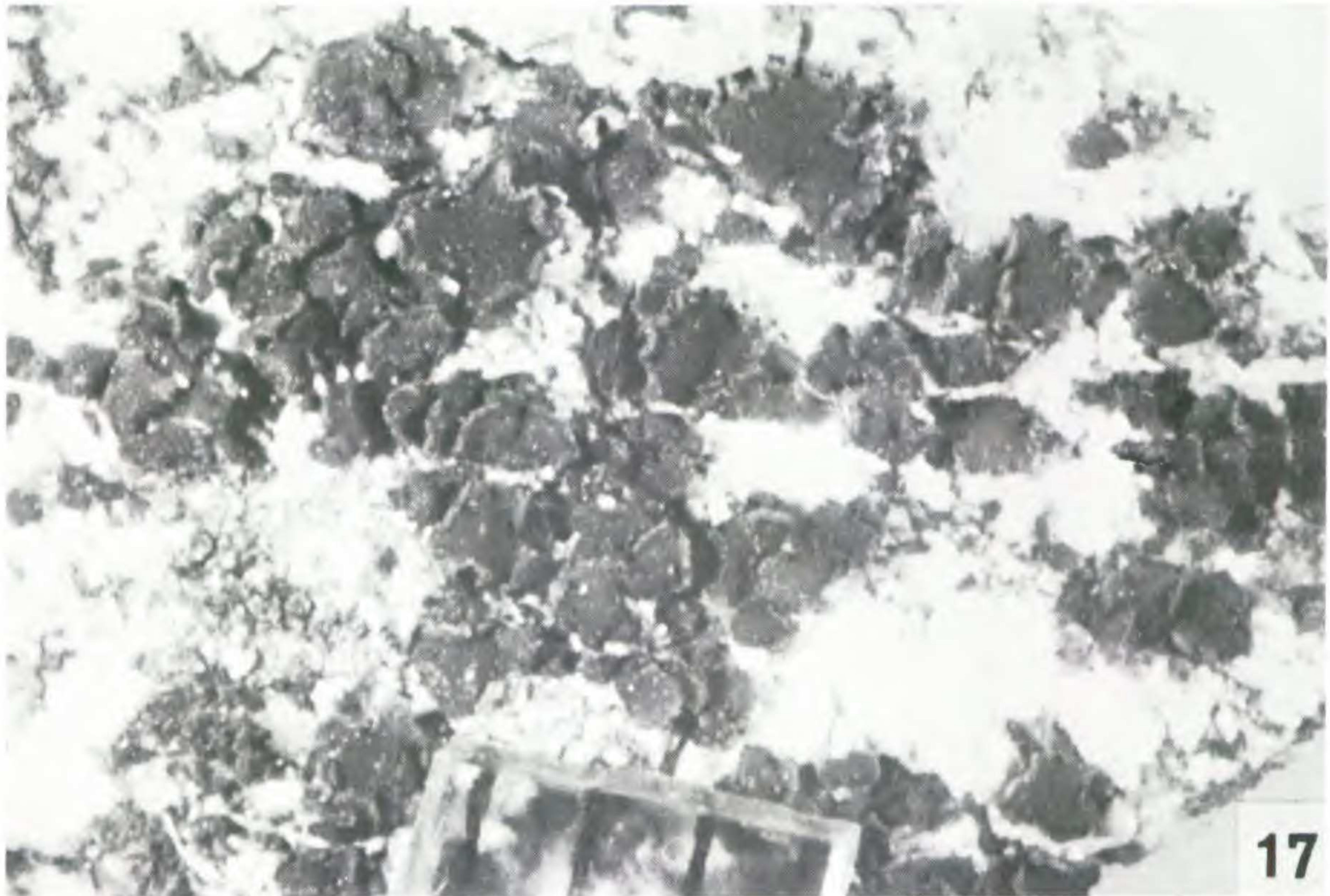
NOMENCLATORIAL REMARKS. The type of *P. radicata* in H-NYL has been examined, and although the algae have not been cultured, the other characters of the recircumscription agree well with *P. radicata*.

*Endocarpiscum*, *Guepinia*, and *Guepinella* were described to separate the polysporous species from the octosporous species, however, *Peltula* was described first. *Heppia* sect. *Placoheppia* was described as a new section for *Heppia placodizans*, however, I do not feel that the differences are significant enough to warrant this separation.

### ***Peltula bolanderi* (Ach.) Wetm., comb. nov.**

*Pannaria bolanderi* Tuck., Gen. Lich. 51, footnote. 1872. *Endocarpiscum bolanderi* (Tuck.) Tuck., Syn. N. Amer. Lich. 1: 114. 1882. *Heppia bolanderi* (Tuck.) Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 215. 1890 (= Étude Lich. Brésil 1: 215. 1890. *Pannariella bolanderi* (Tuck.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 307. 1935. TYPE: California. Ukiah, on rocks, *Bolander* 242. (Holotype FH-TUCKERMAN, isotype FH.)

*Thallus* peltate (Fig. 17), dark olive-brown; squamules small (1–2 mm diameter), lobed and somewhat polyphyllous; margins ascending, undulate, sorediate; attached by umbilicus. *Thallus* lobes 214–336 $\mu$  thick; no upper cortex; lower cortex of several layers of cells, 60–75 $\mu$  thick; medulla of loose hyphae; algal layer 105–150 $\mu$  thick. *Apothecia* rare, 3–8 per squamule, at first totally immersed then sessile with small thalloid rim; discs 0.3–0.5 mm diameter;



FIGURES 17-18.—17. *Peltula bolanderi* (Wetmore 16789). Scale divisions are 1 mm each.—18. *Peltula cylindrica*, lobes broken from thallus (Wetmore 19264). Scale divisions are 1 mm each.

epithecium light yellow, K—; hymenium  $150-170\mu$  thick; paraphyses capitate,  $1.5-3\mu$  thick; asci with gelatinous sheath, containing 100 or more spores; spores ellipsoid to fusiform,  $6.0-7.6 \times 3.0-4.5\mu$ . Hymenium I+ wine-red. Conidia fusiform,  $3.1-3.7 \times 1.2\mu$ .

This species has an Arid Southwestern distribution in North America (Fig. 30) and grows on rock that is usually noncalcareous but also rarely on calcareous rocks or on plant detritus. It occurs in shaded or more moist localities than some *P. euploca*. It frequently occurs in bubble holes on the undersides of large chunks of lava (Fig. 12).

**TAXONOMIC REMARKS.** This species is similar to *P. euploca*, but *P. bolanderi* has upturned lobe margins, is darker in color, smaller, thinner, and has more undulate margins. The apothecia have a small thalloid rim. Some collections from California contain thalli of both species growing side by side and have no intermediates.

Exsiccati: *Plitt, Lich. Exs.* 138 (ABS, FH, MU), 139 (sub *Heppia polyspora*) (ABS, FH). *Zahlbruckner, Lich. Rar.* 90 (FH).

ARIZONA. MARICOPA CO.: Saucedo Mts., 14 miles S of Gila Bend, *Wetmore 14543D*. MOHAVE CO.: W of Burro Creek Crossing, *Darrow*, 1947 (LAM).

CALIFORNIA. COUNTY UNKNOWN: *Bolander* (MICH), *Hasse* (F), Laguna Creek, Santa Cruz Peninsula, *Herre 1233* (DS, FH, NY). ALAMEDA CO.: Oakland Hills, *Bolander 98 p.p.* (FH). INYO CO.: 10 miles N of Independence on US 395, *Wetmore 16757*. LOS ANGELES CO.: *Hasse* (FH, THOMSON). Santa Monica Range, *Hasse*, 1896 (DS); *Hasse*, 1903 (NY); *Hasse*, 1905 (ABS, FH); *Hasse*, 1907 (US); *Hasse*, 1911 (US); *Hasse*, 1912 (ABS); *Hasse*, March, 1915 (FH), *Hasse*, May, 1915 (ABS, FH, MU); Topanga Canyon, *Hasse*, 1907 (NY). 2 miles N of Coldbrook Station along California 39 near Azusa, *Wetmore 16781, 16789, 16802, 16805*. Near San Fernando, *Hasse*, 1908 (FH). Foothills Santa Monica Range near Soldiers Home, *Hasse*, 1911 (LAM). MENDOCINO CO.: Ukiah, *Bolander 242* (FH). MONTEREY CO.: Carmel Valley, Hastings Natural History Reservation, *Tavares 792a* (UC). RIVERSIDE CO.: Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16881C*. San Jacinto Mts., south edge of Banning, *Wetmore 14629 p.p.* (sub *P. euploca*); above Soboba Hot Springs, NE of Hemet, *Wetmore 14702B*. SANTA CLARA CO.: Alum Rock Park, *Baltzo*, 1968 (WETMORE), *Tavares & Baltzo 2268* (WETMORE). SANTA CRUZ CO.: Santa Cruz, *Hasse* (MICH).

NEW MEXICO. SAN MIGUEL CO.: Keary's Gap, W of Las Vegas on road to Mineral Hill, *Wetmore 15152*. UNION CO.: Capulin Mt. National Monument, *Wetmore 15188*. 3 miles N of Capulin Mt. National Monument, *Wetmore 17436*.

UTAH. WASHINGTON CO.: E of Santa Clara along US 91, *Wetmore 17078*.

### ***Peltula clavata* (Kremp.) Wetm., comb. nov.**

*Heterina clavata* Kremp., *Flora* 49: 56. 1876. *Heppia clavata* (Kremp.) Wain., *Acta Soc. Fauna Fl. Fenn.* 7(1): 214. 1890 (= *Étude Lich. Brésil.* 1: 214. 1890). TYPE: Brasil. "Collecti a D. A. Glaziou in provincia brasiliensi Rio Janeiro," ad rupes. (Not seen).

*Thallus* minutely subfruticose, black to greenish-black; lobes 0.5–1 mm long, 0.5–1 mm wide at tips, branched or slightly lobed or sometimes flattened at tips, surface with scattered minute isidia; attached by umbilicus. No cortices present; medulla of loose hyphae with hollow areas; algal layer 25–50 $\mu$  thick. *Apothecia* unknown. *Conidia* fusiform, 3.7–4.3  $\times$  1.2–1.8 $\mu$ .

Only one collection is known from north of Mexico. It was growing on noncalcareous rock probably in a moist habitat (Fig. 30).

**TAXONOMIC REMARKS.** I have only seen a few collections of this species, and therefore the circumscription is provisional. It belongs in *Peltula*, but apothecia must be found to confirm this. The blackish, insidiate thallus helps to distinguish it from other species of *Peltula*.



ARIZONA. COCHISE CO.: Chiricahua Mts., on trail to Silver Peak and Headquarters Gulch, NE of Southwestern Research Station, *Weber, Shushan & Anderson S-24627* (COLO).

Specimens also seen from Mexico and Brasil.

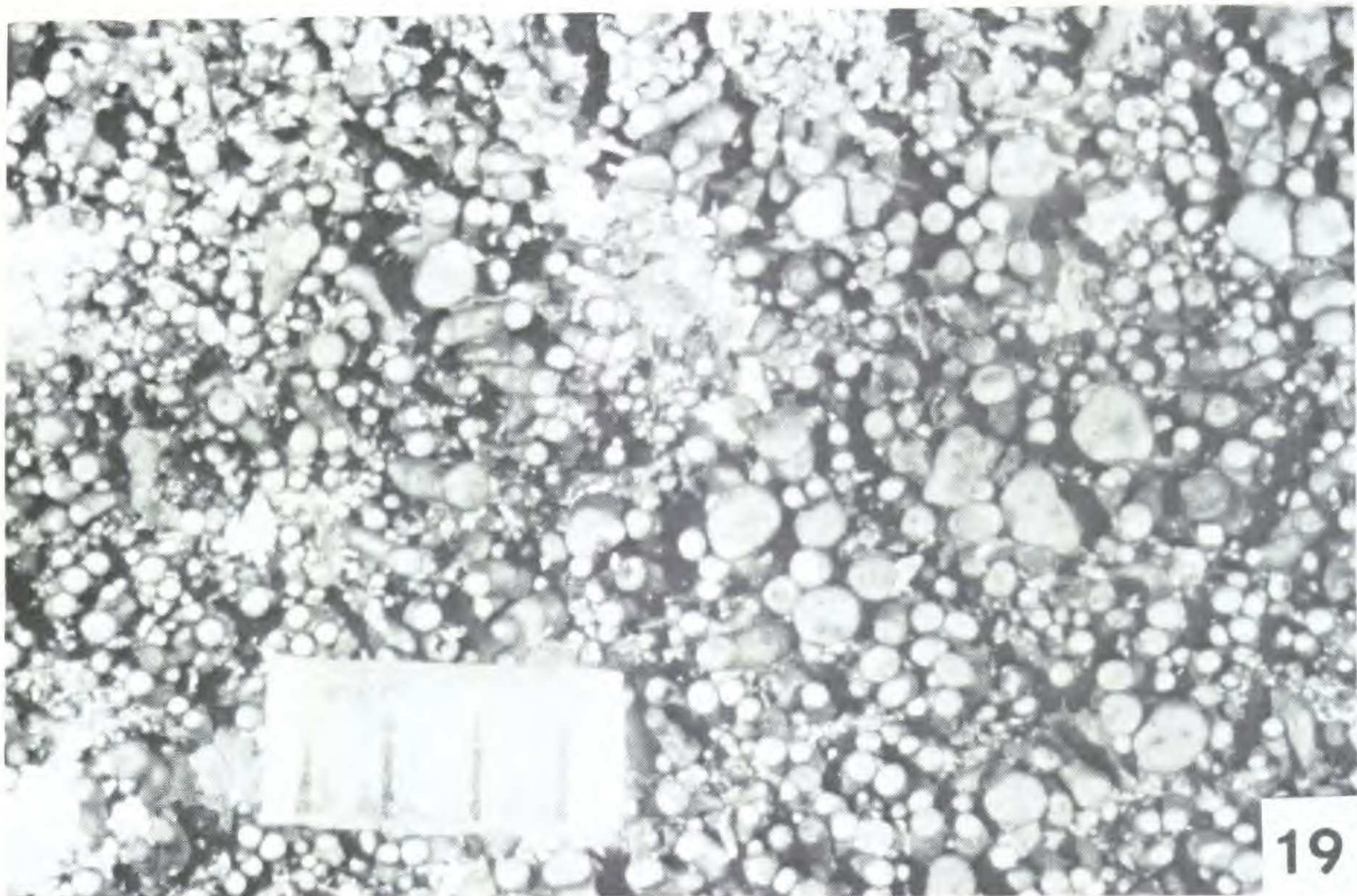
***Peltula cylindrica* Wetm., sp. nov.**

Thallus subfruticulosus, fusco-olivaceus cum crescentibus aspicibus levius pigmentum, formans areas continuas super substratum; lobi cylindrici, recti, aliquanti ramosi, aspices interdum aliquanti complanati, stipes interdum leviter prolificus vel complanatus, juvenillus squamae leviter peltatae, facies laevigata; soredia et insidia desunt; squama affixa per umbilicum. Thalli lobi 296–741 $\mu$  crassi, 0.5–4 mm longi; corticati involuti, cortex paraplectenchymatous, 10–18 $\mu$  crassi, biseriatus vel triseriatus cellularum; cellulae aliquantae rotundati, 4.5–7.6 $\mu$  in diametro; medulla cum laxis hyphis et caveis; stratum algarum involutum, 30–60 $\mu$  crassum; 1–4 cellulae algarum conventae; cellulae 12–18 $\mu$  in diametro; phycobiont *Anacystis*. Lobi fertiles et steriles aequi in magnitudine; apothecia absoluta immersa in apicibus loborum, 1–3 per lobum; disci punctiformes ad 0.1 mm latum; epithecium stramineum, K<sup>-</sup>; hymenium 120–180 $\mu$  crassum, ad 275 $\mu$  in diametro; paraphyses simplices, capitati, 1.8–2.4 $\mu$  crassi; ascus cum vagina gelatinosa, 18–30  $\times$  70–75 $\mu$  continens 100 plus quam spora; spora hyalinae, simplices, globosae, 3.1–4.5 $\mu$  in diametro. Hymenium I<sup>+</sup> vinosum-rubrum, vagina I<sup>-</sup>. Pycnidia immersa in apicibus loborum, 122–214 $\mu$  in diametro; conidia exobasidia, 3.1  $\times$  0.8–1.2 $\mu$ .

*Thallus* subfruticose (Fig. 18–19), olive-brown with growing tips lighter colored, forming continuous areas over substrate; lobes cylindrical, upright, somewhat branched, tips sometimes somewhat flattened, stalk sometimes slightly offset or flattened, very young squamules slightly peltate, surface smooth; non-sorediate, nonisidiate; attached by umbilicus. Thallus lobes 296–741 $\mu$  thick, 0.5–4 mm long; corticate all around, cortex paraplectenchymatous, 10–18 $\mu$  thick, 2–3 layers of cells; cells somewhat rounded, 4.5–7.6 $\mu$  diameter, medulla with loose hyphae and hollow areas (Fig. 3); algal layer all around, 30–60 $\mu$  thick; algae in clumps of 1–4 cells; cells 12–18 $\mu$  diameter; phycobiont *Anacystis*. Fertile lobes same size as sterile lobes; apothecia totally immersed in tips of lobes, 1–3 per lobe (Fig. 6); discs punctiform to 0.1 mm wide; epithecium yellowish, K<sup>-</sup>; hymenium 120–180 $\mu$  thick, to 275 $\mu$  in diameter; paraphyses simple, capitate, 1.8–2.4 $\mu$  thick; asci with gelatinous sheath, 18–30  $\times$  70–75 $\mu$ , containing 100 or more spores; spores hyaline, nonseptate, globose, 3.1–4.5 $\mu$  diameter. *Hymenium* I<sup>+</sup> wine-red, sheath I<sup>-</sup>. *Pycnidia* immersed in tips of lobes, 122–214 $\mu$  diameter; conidia exobasidial, 3.1  $\times$  0.8–1.2 $\mu$ .

Type: GEORGIA. DEKALB CO.: 20 miles E of Atlanta on Mt. Arabia, *Wetmore 19264*, 1969. [Holotype in my herbarium, Isotypes to be widely distributed (over 100 packets)].

TAXONOMIC REMARKS. This species is similar to *Peltula tortuosa*, but it has more terete lobes, the fertile lobes are the same size as vegetative lobes, and the ascus has a gelatinous sheath. *Peltula zahlbruckneri* is more peltate, has no



FIGURES 19-20.—19. *Peltula cylindrica* (Wetmore 19264). Scale divisions are 1 mm each.—20. *Peltula euploca* (Wetmore 17394). Scale divisions are 1 mm each.

algae in the stalk of the lobes, has shorter stalks, and the lobes are more flattened and broad.

This species was first brought to my attention by Mrs. Joan Jones as a result of her studies in the Atlanta, Georgia area. She has been kind enough to supply

me with notes on the occurrence and ecology of this lichen. Most of what follows comes from her notes supplemented by my field observations.

*Peltula cylindrica* has been collected on five granitic outcrops within 30 miles of Atlanta: Stone Mountain, Mount Arabia, Panola Mountain, Rollaway, and Rock Chapel outcrops (Fig. 30). It is most abundant on Mt. Arabia where it covers large areas (Fig. 10–11). The average annual precipitation in the Atlanta area is 47.14 inches. *Peltula cylindrica* grows on sloping and flat rock and is abundant in fairly steep drainage paths and shallow rock depressions. In these drainage paths it is frequently wet with runoff and dries soon after the rain. The rock depressions dry within a few days after a rain. It has not been found in places where there is a persistent seepage. It is more abundant on west and southwest slopes.

Henssen also studied some material of this species, and her comments are included under *Heppia tortuosa* (Henssen, 1970).

GEORGIA. DEKALB CO.: Mt. Arabia, Jones, 1969 (WETMORE), Wetmore 19264. Panola Mt., Jones, 1968 (WETMORE). Stone Mt., 14 miles E of Atlanta, Wetmore 19262.

***Peltula euploca* (Ach.) Wetm., comb. nov.**

*Lichen euplocus* Ach., Lich. Suec. Prod. 141, 1798. *Heppia euploca* (Ach.) Vain., Acta Soc. Fauna Fl. Fenn. 49(2): 14, 1921. TYPE: Sweden, Westring (H, not seen.)

*Endocarpon guepinii* Del. in Duby, Bot. Gall. ed. 2, 2: 594, 1830. *Endocarpiscum guepinii* (Del. in Duby) Nyl., Flora 47: 487, footnote, 1864. *Dermatocarpon guepinii* (Del. in Duby) Tuck., Lich. Calif. 28, 1866. *Pannaria guepinii* (Del. in Duby) Tuck., Gen. Lich. 51, 1872. *Heppia guepinii* (Del. in Duby) Nyl. in Hue, Rev. Bot. Bull. Mens. 5: 18, 1886 (= Add. Lich. Eur. 1: 62, 1886). *Peltula guepinii* (Del. in Duby) Gyel., Repert. Spec. Nov. Regni Veg. 38:308, 1935. *Guepinia polyspora* Hepp, Verh. Schweiz. Naturf. Ges. 48: 85, 1864 and Bot. Zeit. 22 (Beibl.): 11, 1864. *Guepinella myriocarpa* Bagl., Nuovo Giorn. Bot. Ital. 2: 175, 1870. TYPE: France. "Ad rupes schistaceos humidus ad meridiem versos in agro Andegavensi, Guepin." (Not seen.)

*Heppia polyphylla* B. de Lesd., Ann. Cryptog. Exot. 5(2): 113, 1932. TYPE: New Mexico. Las Vegas, Soldier's Camp, Arsène 19910. (Lectotype US; isotypes FH, MSC.)

*Heppia dermatocarpea* Räs., Anales Soc. Ci. Argent. 128: 145, 1939. TYPE: Uruguay. Montevideo, Barra, saxicola, Herter, 1933 (Holotype H.)

NOMENCLATORIAL REMARKS. Wainio (1921) selected the material from Sweden as the type of *Lichen euplocus* Ach. I have seen photographs of this material, and the identification seems to be correct.

*Guepinia polyspora* Hepp was proposed as a *nomen novum* for *Endocarpon guepinii*. Hepp found that the asci contained about 100 spores and so could not remain in *Endocarpon*.

*Guepinella myriocarpa* Bagl. was proposed as a *nomen novum* for *Endocarpon guepinii*.

The holotype of *Heppia polyphylla* B. de Lesd. has probably been destroyed. I select the isotype in US as lectotype.

The holotype of *Heppia dermatocarpea* Räs. is identical with other monophyllous material of *Peltula euploca* from other parts of the world.

*Thallus* peltate (Fig. 20), tan olive-green; squamules 3–10 mm diameter, lobed and polyphyllous or only slightly notched or entire; margins thicker, down-

rolled, not undulate, sorediate; attached by umbilicus. Thallus 214–367 $\mu$  thick, no upper cortex; lower cortex of several layers of rounded cells in 7–10 rows, 50–90 $\mu$  thick; medulla of loose hyphae; algal layer 75–150 $\mu$  thick (Fig. 2). *Apothecia* many per squamule, totally immersed; discs punctiform or expanded to 0.7 mm, no thalloid rim; epithecium yellowish-brown, K<sup>-</sup>; hymenium 105–220 $\mu$  thick, often pinkish; paraphyses capitate, 1.5–3.0 $\mu$  thick; asci with gelatinous sheath, 100–120  $\times$  21–27 $\mu$ , containing 100 or more spores; spores ellipsoid to fusiform, 6.0–7.6  $\times$  3.0–4.5 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* fusiform, 3.4  $\times$  1.5 $\mu$ .

*Peltula euploca* has an Arid Southwestern distribution in North America with a few outliers (Fig. 31). It occurs on noncalcareous rock in both very dry habitats and in shady areas of rock which are probably subject to intermittent water flow (Fig. 9).

**TAXONOMIC REMARKS.** Sometimes the umbilicus of this species and *P. bolanderi* may begin growing after the main thallus has been broken off. In these cases the regenerated growth may resemble that of normal *P. placodizans*. Occasionally young thalli may not have well developed soralia and separation of these from *P. omphaliza* is difficult unless apothecia are present. A few pruinose specimens were seen but this species is usually epruinose.

ALABAMA. COUNTY UNKNOWN: Locality unknown, *Peters*, 1883 (FH).

ARIZONA. COCONINO CO.: 2 miles N of Flagstaff in Rio de Flag Canyon, *Shushan & Johnson S-14851* (SHUSHAN). COCHISE CO.: Chiricahua Mts., Stewart Campground between Portal and the forks of Cave Creek, *Weber, Shushan & Anderson S-24659* (COLO); W of Portal on trail from Rustler's Park to Fly's Peak, *Weber & Shushan S-8987* (COLO). GRAHAM CO.: Coronado National Forest, above Stockton Pass Campground, S of Safford, *Wetmore 14466, 14499*. PIMA CO.: Tumamoc Hill, west outskirts of Tucson, *Weber L-36747* (COLO). Tucson Mts., *Darrow 1309* (COLO).

ARKANSAS. COUNTY UNKNOWN: Ozark Mts., *Peters*, 1876 (FH).

CALIFORNIA. COUNTY UNKNOWN: Santa Cruz Mts., *Hasse* (MICH). Mt. Hamilton Road, *Herre 75* (DS). Near Ocean View, *Howe*, 1893 (NY). ALAMEDA CO.: Oakland Hills, *Bolander*, before 1870 (FH). KERN CO.: 2.7 miles N of Caliente, *Tavares & Brinson 1169b, 1169c* (both UC). LAKE CO.: 2 miles S of Lucerne, along Clear Lake, *Cooke 16704* (F). LOS ANGELES CO.: San Gabriel Mts., *Hasse*, 1897 (ABS); Rubio Canyon, *Kingman*, 1911 (FH). San Gabriel Canyon, *Hasse*, 1902 (POM). 2 miles N of Coldbrook Station along California 39 between Crystal Lake Campground and Azusa, *Wetmore 16780, 16798*. Santa Monica Mts., *Hasse* [6 specimens collected between 1890 and 1911] (FH, LAM, NY, POM, US); Topanga Canyon, *Hasse*, 1906 (FH); NW of Topanga in Old Topanga Canyon, 2.5 miles off Topanga Canyon Road, *Wetmore 16828*. Santa Catalina Island, *Hasse*, 1906 (FH); Silver Canyon, *Nuttall 450* (F, FH); east end of Whites Cove at headland point (Bible Peak), *Weber & Santesson L-42802* (COLO). San Clemente Island, west-trending canyon running seaward toward Lost Point, *Weber & Santesson L-42879* (COLO). MARIN CO.: Mill Valley, *Herre*, 1930 (F, LAM). 2.5 miles SE of Stinson's Beach, *Brown*, 1942 (F, LAM). MONTEREY CO.: Monterey, *Farlow* (FH). Hastings Reservation, *Linsdale 188* (F). RIVERSIDE CO.: Elsinore, *Hasse*, 1888 (FH). San Jacinto Mts., at S edge of Banning, *Wetmore 14629*; above Palm Desert, *Wetmore 14584, 14594*; at west edge of Palm Springs in Chino Canyon, *Wetmore 14613*; above Soboba Hot Springs (NE of Hemet), *Wetmore 14699, 14702A*. In Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16885B, 16896*. Along California 71 a few miles NE of junction with California 79, *Wetmore 16903*. S of Riverside near Perris, *Wetmore 14725*. Palm Springs, *Hasse FN 816* (FH). SAN BERNARDINO CO.: Along US 66 SW of Barstow 29 miles, on Wells-Stoddard Road, *Wetmore 17023*. Joshua Tree National Monument, near Hidden Valley Campground, *Wetmore 16901*. 10 miles S of Needles, *Drouet & MacBride 4683* (F). SAN DIEGO CO.: W of Anza-Borrego State Park on county highway S2 between California 79 and California 78,

*Wetmore* 16948. San Diego, *Farlow*, 1885 (PH), *Orcutt* (FH). San Diego at "Atlantus Restaurant" in Mission Bay Park, *Wetmore* 17020. Otay, *Orcutt* 124 (US). Along back road between California 94 and Chula Vista near Otay Reservoir, *Wetmore* 17018. 6.8 miles SE of Temecula on road to Pala, *Tavares & Brinson* 1106a (UC). SAN MATEO CO.: S of Pasadena, *Cain* 26156 (TRTC). On rocks on sea coast, *Bolander*, 1864 or 1865 (F). Pigeon Point, *Herre* [8 specimens collected between 1932 and 1957] (F, LAM, NY, TRTC, US); lighthouse, *Shushan* S-14679 (COLO, US); 1 mile S of lighthouse, *Doty* 5427 (F, PH, WIS). Santa Cruz Mts. near Pt. San Pedro, *Herre* 499 (DS, FH, MINN, NY, US); Stony Point, Searsville Ridge, *Herre* 140 (DS, FH, MINN, NY); hills near Stanford University, *Herre* 149 (MU, UC); Stevens Creek Canyon, *Herre* 613 (DS, FH, MINN, MO). Searsville Lake, 6 miles from Stanford University, *Shushan* 11094 (COLO). Santa Cruz, *Hasse* (MICH). Alum Rock Park, *Herre* 42 (DS). SONOMO CO.: Danell Estate, Sonoma Valley, *Roderick*, 1961 (UC). 1 mile N of Santa Rosa, *Brown* 439 (LAM). VENTURA CO.: Locality and collector unknown, [*Hasse?*], 1903 (FH).

COLORADO. COUNTY UNKNOWN: Locality unknown, *Brandege* (FH, MICH, US). ALAMOSA CO.: Great Sand Dunes National Monument, 25 miles NE of Alamosa, *Shushan* Sl-5294 (SHUSHAN). BOULDER CO.: Boulder Canyon, vicinity of Boulder Falls, *Weber & Persson* Sl-292 (COLO), *Shushan* Sl-377 (SHUSHAN). Summit of Flagstaff Mt., W of Boulder, *Weber & Imshaug* S-9930 (COLO), *Wetmore* 15783. Dakota Ridge W and NW of Boulder, *Anderson* S-20209 (COLO), *Anderson* S-20113 (COLO); Rabbit Mt., 4 miles NE Lyons of above Little Thompson River, *Anderson* S-20441 (COLO, DUKE, FH, MSC). South St. Vrain Canyon, 5.5 miles W of Lyons, *Weber, Santesson & Anderson* L-41951 (COLO, WETMORE). 2.5 miles NW of Lyons along North St. Vrain Creek near mouth of canyon, *Wetmore* 16205, 16221. West base of Steamboat Mt., 2 miles NW of Lyons, *Shushan & Weber* S-18591 (COLO). CONEJOS CO.: 1 mile E of Manassa, *Wetmore* 17287. EL PASO CO.: North Cheyenne Canyon, Colorado Springs, *Jeanett*, 1913 (ABS). GRAND CO.: Rocky Mt. National Park, 1 mile E of Grand Lake, base of south slope of Mt. Enentah, *Anderson* 3432 (COLO); NE of Grand Lake between Summerland Park and Cascade Falls of North Inlet, *Anderson* 3240 (COLO, WETMORE). JEFFERSON CO.: Along US 6, 14 miles E of Idaho Springs in Clear Creek Canyon W of Denver, *Wetmore* 16243. Clear Creek Canyon 8 miles SE of Pinecliffe, *Shushan* Sl-893 (SHUSHAN). LARIMER CO.: Dakota Ridge, 22 miles N of Ft. Collins, 2 miles SE of Table Mt., *Anderson* S-20154 (COLO); 4.5 miles SW of Ft. Collins, just above Horsetooth Reservoir, *Anderson* S-20291 (COLO). Rocky Mt. National Park, SW slope of Deer Mt., *Anderson* 3573 (COLO); Fall River Canyon, 1 mile W of Endovalley Campground near Chasm Falls along Fall River, *Anderson* 1941 (COLO). Gem Lake Trail, 2 miles NE of Estes Park, *Shushan, Anderson & Sims* Sl-3345 (SHUSHAN). 0.5 mile S of Wyoming state line, just N of Virginia Dale, *Shushan* Sl-90 (SHUSHAN). LOGAN CO.: 7 miles N of Westplains, 27 miles NW of Sterling, *Shushan* Sl-335 (SHUSHAN).

MARYLAND. WASHINGTON CO.: Harper's Ferry, *Tuckerman*, 1852 (FH, MICH, US).

MASSACHUSETTS. NORFOLK CO.: Needham, *Tuckerman*, 1844 (FH).

MINNESOTA. RENVILLE CO.: Morton, *Fink* 322 (MICH, MINN, MU).

NEVADA. CLARK CO.: Mt. Diablo baseline and meridian, Las Vegas, *LePak* vv-194 (COLO). On road to Mormon Mesa, 6.5 miles N of junction with highway 91, about 14 miles W of Mesquite, *Tavares* 1516a (UC).

NEW MEXICO. BERNALILLO CO.: Arroyo San Antonio, 2 miles above junction of highway 66 and Sandia Loop Drive, *Shushan & Weber* S-6852 (COLO, DUKE, FH, MSC). SAN MIGUEL CO.: Las Vegas, Soldier's Camp, *Arsène* 19910 (FH, MSC, US), 19890, (FH, US). 28 miles SW of Las Vegas, 2.5 miles W of Sands, *Shushan* S-11126 (COLO). Kearny's Gap, W of Las Vegas on road to Mineral Hill, *Wetmore* 15152 p.p. (sub *P. bolanderi*). SOCORRO CO.: Magdalena Mts., just S of highway 5 miles SW of Socorro, *Shushan & Weber* S-6927 (COLO, FH, MSC, US, WIS, WTU). UNION CO.: 3 miles N of Capulin Mt. National Monument, *Wetmore* 17394. 7 miles E of Folsom, *Shushan* S-11435 (COLO).

SOUTH DAKOTA. MEADE CO.: 2.5 miles E of Piedmont Butte, 23 miles ESE of Lead, *Wetmore* 10369 (MSC, WETMORE). PENNINGTON CO.: Along Pine Creek at head of Horse Thief Lake, 18 miles SW of Rapid City, *Wetmore* 10962 (MSC).

TEXAS. BREWSTER CO.: Big Bend National Park, South Rim Trail to Emory Peak, Chisos Mts., *Anderson & Shushan* S-18693 (COLO); Boulder Meadows, *Wetmore* 18492; Grapevine Hills NW of Headquarters, *Wetmore* 18287A, 18293A; Green Gulch, *Wetmore* 18437B; Pine Canyon, *Wetmore* 18422.

UTAH. WASHINGTON CO.: 8 miles E of St. George on west bank of Virgin River, *Shushan S-14606* (COLO). 0.5 mile E of Santa Clara along US 91, *Wetmore 17079*.

WASHINGTON. KITTITAS CO.: 20 miles NW of Wymer, *James, 1969* (WETMORE).

Specimens also seen from Mexico, Argentina, Uruguay, Hawaii, Australia, and Europe.

***Peltula michoacanensis*** (B. de Lesd.) Wetm., comb. nov.

*Heppia michoacanensis* B. de Lesd., Lich. Mexique 10. 1914. TYPE: Mexico. État de Michoacán, Morelia, lomas à l'ouest du Zapote, *Arsène 3813, 1910*. (Lectotype US; isotypes DUKE, FH, WIS).

NOMENCLATORIAL REMARKS. The holotype has probably been destroyed, so I am selecting the isotype in US as lectotype.

*Thallus* squamulose (Fig. 21), tan-olive; squamules 1–2 mm diameter, shallowly or deeply lobed, concave and cone shaped; margins ascending; attached by central branched umbilicus. Thallus 150–350 $\mu$  thick; upper cortex not developed; lower cortex of 3–5 layers of rounded cells, 25–50 $\mu$  thick; medulla variable but usually cellular at lobe margins and with agglutinate hyphae in center near umbilicus with some loose hyphae; algal layer 73–130 $\mu$  thick, algal cells in vertical rows. *Apothecia* one per squamule, immersed in center of concave squamule; discs 0.5–1 mm diameter, without thalloid rim, not filling squamule; epithecium light brown, K<sup>-</sup>; hymenium 150–220 $\mu$  thick; paraphyses 1.7 $\mu$  thick; asci with gelatinous sheath, containing 100 or more spores; spores ellipsoid to fusiform, 6.1–7.7  $\times$  3.4–4.6 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* bacilliform, 3.1–3.7  $\times$  1.2–1.8 $\mu$ .

This species is very rare north of Mexico but probably much more abundant in Mexico (Fig. 32). It grows on a thin layer of soil over calcareous or non-calcareous rock.

TAXONOMIC REMARKS. The squamules are larger and cone-shaped in this species as opposed to the smaller, flat or convex squamules in *P. obscurans* var. *deserticola*. The umbilicus in *P. michoacanensis* is much larger.

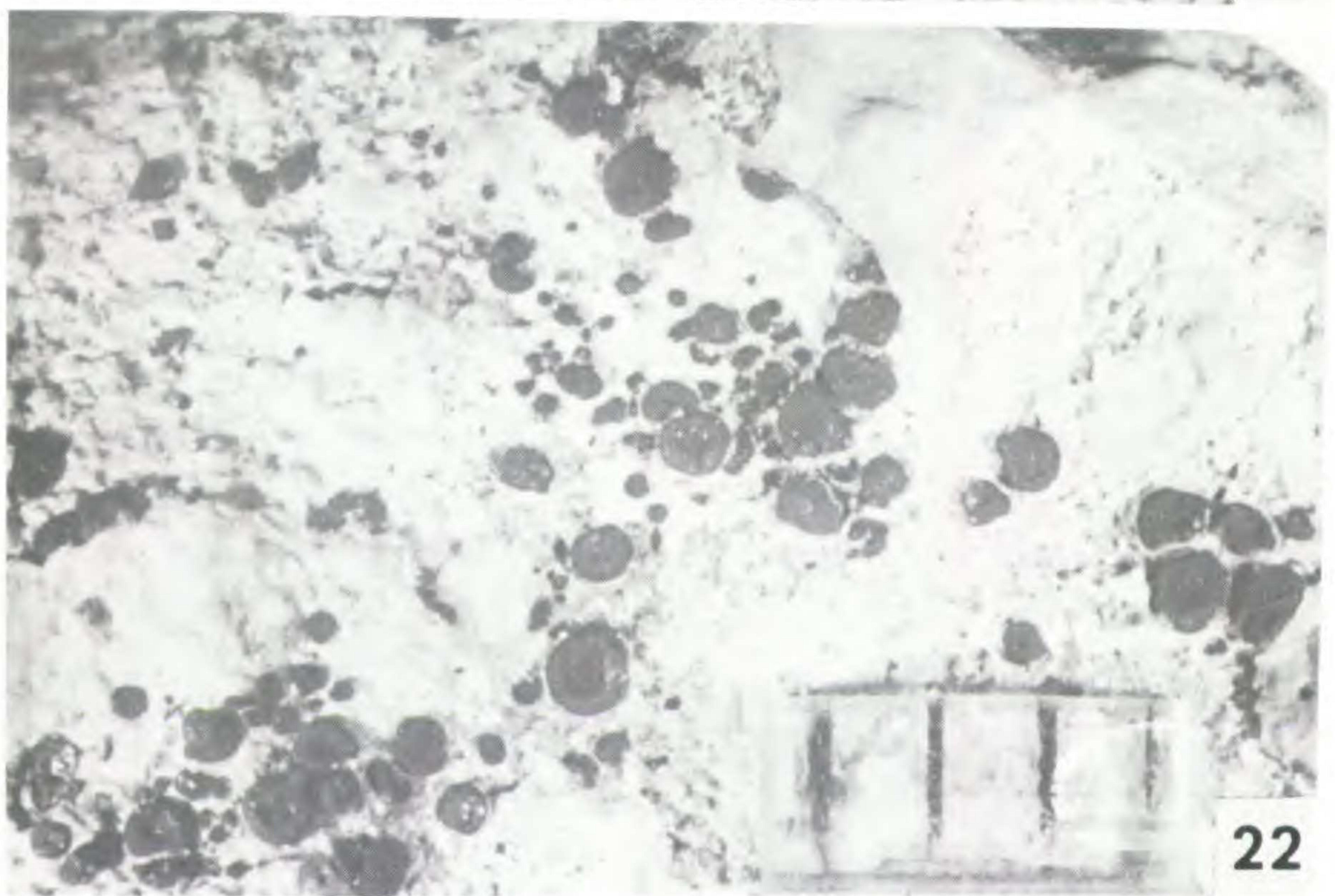
CALIFORNIA. RIVERSIDE CO.: San Jacinto Mts., above Palm Desert, *Wetmore 14595*; above Soboba Hot Springs, NE of Hemet, *Wetmore 14704*.

Specimens also seen from Mexico and one from India which may belong to this species.

***Peltula obscurans*** (Nyl.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 308. 1935.

*Endocarpiscum obscurans* Nyl., Bull. Soc. Linn. Normandie II. 6: 309. 1872. *Heppia obscurans* (Nyl.) Nyl. in Hue, Rev. Bot. Bull. Mens. 5: 18. 1886 (= Add. Lich. Eur. 1: 62. 1886). *Heppia guépinii* var. *obscurans* (Nyl.) Boist., Nouv. Fl. Lich. 2: 87. 1903. TYPE: France. Collioure, *Nylander, 1872* (Lectotype H-NYLANDER, Herb. 30900).

*Heppia deserticola* f. *minor* Zahlbr., Ann. Mycol. 7: 474. 1909. TYPE: Arizona. Tucson, on rocks, *Blumer, 1908*. (Holotype not found; isotypes MICH, MU).



FIGURES 21-22.—21. *Peltula michoacanensis* (Wetmore 14595). Scales divisions are 1 mm each.—22. *Peltula obscurans* var. *deserticola* (Wetmore 15141). Scale divisions are 1 mm each.

NOMENCLATORIAL REMARKS. Among the original collections in Nylander's herbarium in Helsinki are two that could be considered for the types. One of these (H-NYL 30900) agrees well with the type description, and I have selected it as lectotype. The other (H-NYL 30897) was selected by Gyelnik (1935) as

lectotype, but the collection I saw from Helsinki has nothing like this species in it and is all *Peltula euploca*.

The holotype of *Heppia deserticola* f. *minor* Zahlbr. could not be found in Vienna. Since it may be found in another herbarium, I have not selected a lectotype but based the identification on the isotypes.

**TAXONOMIC REMARKS.** This is a very variable species. The cortical development and the type of medulla vary somewhat with the pH of the substrate. Specimens from calcareous substrates have less well developed cellular tissues than those from noncalcareous substrates, and lobing of the thallus is more pronounced on noncalcareous substrates. Since there are a few rare intermediates between the otherwise distinct types, I have recognized the following varieties based on thallus variations and epithecium reactions.

### ***Peltula obscurans* var. *obscurans***

*Thallus* squamulose, brownish-olive to greenish-olive; squamules 0.2–2 mm diameter, lightly to deeply lobed, flat to convex; attached by branched umbilicus. Thallus 183–244 $\mu$  thick; upper cortex not developed; lower cortex usually present but not distinguishable from the medulla; medulla cellular or rarely with loose hypae; algal layer 91–183 $\mu$  thick. *Apothecia* one per squamule, at first immersed but finally emergent with thin thalloid rim; disc 0.3–0.8 mm diameter; epithecium yellowish-brown, K<sup>+</sup> red-violet; hymenium 70–150 $\mu$  thick; paraphyses 1.5–3.0 $\mu$  thick; asci with gelatinous sheath, 52–75  $\times$  15–18 $\mu$ , containing 100 or more spores; spores ellipsoid to oval, 4.5–7.6  $\times$  3.0 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* oval-fusiform, 3.1–3.7  $\times$  1.2 $\mu$ .

This variety probably has an Arid Southwestern distribution but has only been found along the southern border of the United States (Fig. 33). It will probably be found in Mexico after more collecting is done there. It usually grows on rock but occasionally on soil. The substrates are usually noncalcareous. It grows in open, dry, rocky deserts.

**TAXONOMIC REMARKS.** The lectotype collection of the species has the K<sup>+</sup> red reaction in the hymenium. This variety has thallus variations similar to the other varieties but has the K<sup>+</sup> red-violet epithecium. This is the rarest variety in spite of being the typical variety nomenclaturally.

Exsiccati: *Plitt, Lich. Exs.* 35 (sub *Heppia hassei*) (ABS, F).

ARIZONA. COCHISE CO.: Chiricahua Mts., Cave Creek Canyon, 3 miles N of Portal, *Weber & Shushan* S-8839 (COLO). MARICOPA CO.: N of Gila Bend on US 80, *Wetmore* 14533A. PIMA CO.: Tucson, *Blumer*, 1908 (MICH, MU), *Darrow* 572 (COLO). Saguaro National Monument, NW of Tucson, *Wetmore* 14514A, 14518B.

CALIFORNIA. LOS ANGELES CO.: Santa Monica Range, *Hasse*, 1902 (US), 1908 (ABS). Santa Monica Hills near Sawtelle, *Hasse*, 1908 (F). RIVERSIDE CO.: San Jacinto Mts., above Palm Desert, *Wetmore* 14577. Palm Springs, *Hasse*, 1903 (NY, POM), 1904 (MICH).

NEVADA. CLARK CO.: 14 miles W of Mesquite, on road to Mormon Mesa, *Tavares* 1509, 1516d (both UC).

NEW MEXICO. DONA ANA CO.: Organ Mts., 15 miles E of Las Cruces near San Agustin Pass along US 70, *Wetmore* 14442B.

TEXAS. BREWSTER CO.: Big Bend National Park, Green Gulch, *Wetmore* 18445; 2 miles from highway on road to Grapevine Hills, *Wetmore* 18294A. UPTON CO.: North of McCamey in King Mt. area, *Wetmore* 14240.

Specimens also seen from Mexico, Peru, France, and Italy.



***Peltula obscurans* var. *deserticola* (Zahlbr.) Wetm., comb. nov.**

*Heppia deserticola* Zahlbr., Bull. Torrey Bot. Cl. 35: 300. 1908. TYPE: Arizona. Tucson, southward facing tuff, station III, *Blumer*, 1908. (Holotype not found; isotype MICH.)

*Heppia michoacanensis* var. *adnata* B. de Lesd., Lich. Mexique, 1 Suppl. 8. 1922, processed publication. TYPE: Mexico. Michoacán, Azotea de San Borja, Arsène 9604, 1914. (Lectotype US; isotype DUKE.)

NOMENCLATORIAL REMARKS. The holotype of *Heppia deserticola* Zahlbr. could not be found in Vienna, but since it may later be found I have not selected a lectotype. I have based my interpretation on the isotype.

*Heppia michoacanensis* var. *adnata* B. de Lesd. was described in a mimeographed paper and so was not validly published. I have not found a later valid publication. The holotype has probably been destroyed, and I am selecting the isotype in US as the lectotype.

*Thallus* squamulose (Fig. 22), olive-brown; squamules 0.5–1.2 mm diameter, not lobed or only slightly so, convex or flat; attached by clump of rhizines or umbilicus. Squamules 105–240 $\mu$  thick; upper cortex not developed; lower cortex poorly developed or not present; medulla of loose hyphae or with rare cellular areas; agal layer 60–120 $\mu$  thick. *Apothecia* one or two per squamule, immersed and finally filling the whole squamule leaving squamule margin as the rim (Fig. 5); disc 0.3–1.2 mm diameter, epithecium yellowish-brown, K<sup>-</sup>; hymenium 105–140 $\mu$  thick; paraphyses 1.5–3.0 $\mu$  thick; asci with gelatinous sheath, 60–75  $\times$  19–27 $\mu$ , containing 100 or more spores; spores ellipsoid to oval, 4.6–7.7  $\times$  3.0–4.6 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* fusiform, 3.1–3.7  $\times$  1.2–1.8 $\mu$ .

This variety has an Arid Southwestern distribution (Fig. 34) and is very abundant in dry semi-desert and desert areas (Fig. 14). In many areas it occurs on almost all pebbles in the area, however, since it is small, it has been rarely collected. It usually occurs on calcareous rock.

TAXONOMIC REMARKS. The degree of development of the cellular tissue of the thallus is better on noncalcareous rocks. See further notes under the species.

Exsiccati: *Plitt, Lich. Exs.* 138 (sub *Heppia bolanderi*) (DS).

ARIZONA. COCHISE CO.: Near Portal, E of Chiricahua Mt. base, *Roth*, 1963 (COLO). COCONINO CO.: Grand Canyon, Bright Angel Trail, *Hasse*, 1904 (NY); South Rim, Hermit's Rest trail, *Wetmore* 14985B, 14986; South Rim, Rowes Well Road, *Wetmore* 15016. 25 miles S of Grand Canyon on US 180, *Wetmore* 14932. MARICOPA CO.: N of Gila Bend near Buckeye on US 80, *Wetmore* 14532. Saucedo Mts., 14 miles S of Gila Bend along Arizona 85, *Wetmore* 14542. Pinnacle Peak Pass, 4 miles from Verde River near Scottsdale, *Weber & McCleary* S-1929 (COLO). NAVAJO CO.: 10 miles E of Winslow on US 66, *Wetmore* 15045. PIMA CO.: Tucson, *Blumer*, 1908 (MICH, MU). Tumamoc Hill, west outskirts of Tucson, *Weber* L-36749, L-37649, L-36755 (all COLO, WETMORE). Tucson Mts., *Darrow* 746 (WIS). Saguaro National Monument NW of Tucson, *Wetmore* 14514C. Near Pantano, SW of Tucson on US 80, *Wetmore* 14511, 14512. Organ Pipe Cactus National Monument below headquarters. *Sierk* 2285 (SIERK). PINAL CO.: Picacho Pass NW of Tucson along Interstate 10, *Wetmore* 14520, 14522. YAVAPAI CO.: 6 miles W of Ash Fork on US 66, *Wetmore* 14924. Along Arizona 279 SE of Cottonwood, *Wetmore* 15041. YUMA CO.: Near Mohawk E of Yuma on US 80, *Wetmore* 14546.

CALIFORNIA. INYO CO.: Death Valley National Monument, NE of Stovepipe Wells, *Wetmore* 14879. LOS ANGELES CO.: Santa Monica Mts., *Hasse* FN 917 (FH), 1915 (DS); Sullivan's Canyon, *Hasse*, 1913 (FH); Topanga Canyon at "4 Oaks," *Hasse* (FH). Catalina

Island, *Hasse FN 1400* (FH) 1911 (FH). RIVERSIDE CO.: S of Cathedral City, *Wetmore 16870*. Near western edge of Palm Desert, *Wetmore 16851*.

COLORADO. BOULDER CO.: Between Altona and Lyons, 0.5 mile S of Summit Red Hill, *Shushan & Weber 3368* (COLO). West base of Steamboat Mt., 2 miles NW of Lyons, *Shushan & Weber S-17936* (COLO). 1.5 miles NW of Lyons on Steamboat Mt., *Wetmore 16125, 16173, 16176A, 16182*.

KANSAS. CHASE CO.: Locality unknown, *Hall 14* (FH).

NEVADA. CLARK CO.: Along US 91 NE of Las Vegas, 22 miles at road going to Axial, *Wetmore 17042*. Near Gold Butte, *Tavares 31f* (UC). Virgin River, 2.5 miles NE of Mesquite, *Tavares 473a* (UC). Road to Mormon Mesa, 14 miles from Mesquite, *Tavares 1253, 1507, 1516* (UC). NYE CO.: Near Mercury, along US 95, *Wetmore 14889A*.

NEW MEXICO. EDDY CO.: Near Hope, 21 miles W of Artesia along US 82, *Wetmore 14319B, 14321*. LUNA CO.: Near Gage, 19 miles W of Deming on US 70, *Wetmore 14459*. MCKINLEY CO.: Along US 66 at road to Manvelito, 13 miles W of Gallup, *Wetmore 15065, 15090*. SAN DOVAL CO.: N of Albuquerque on road to Placitas, *Wetmore 15141, 15142*. SAN MIGUEL CO.: Kearny's Gap, W of Las Vegas on road to Mineral Hill, *Wetmore 15169*.

OKLAHOMA. GARFIELD CO.: 3 miles SW of Douglas by Wolf Creek, *Keck 268* (KECK). MURRAY CO.: Platt National Park, *Wetmore 14122B*. TEXAS CO.: 7 miles NE of Guyman on US 54, *Wetmore 15225*.

TEXAS. BREWSTER CO.: Big Bend National Park, below Burro Mesa Pourouff, *Wetmore 18312B*; Dagger Flats, *Wetmore 18208*; 2 miles W of junction with road to Castolon, *Wetmore 18302*; Grapevine Hills NW of headquarters, *Wetmore 18288*; 2 miles from highway on road to Grapevine Hills, *Wetmore 18294B*; Green Gulch, *Wetmore 18430*; Hot Springs near Rio Grande Village, *Wetmore 18187, 18192*; 4 miles W of junction of main road and road to Basin Campground, *Wetmore 18295A*; Old Mine Road near Rio Grande Village, *Wetmore 18379*; 7 miles W of junction with road to Basin Campground, *Wetmore 18296*; W of junction going to Santa Elena Canyon along Texas 170, *Wetmore 14304, 14307*; at junction of US 385 and Texas 2627, 40 miles from Park headquarters, *Wetmore 14246*. BROWN CO.: SW of Brownwood on US 67, *Wetmore 14217*. UPTON CO.: N of McCamey in King Mt. area, *Wetmore 14232*.

UTAH. EMERY CO.: Along US 6, 27 miles S of Price, *Wetmore 16519A*. GRAND CO.: Along US 6, 2 miles E of Green River, *Wetmore 16503*.

Specimens also seen from Mexico.

***Peltula obscurans* var. *hassei* (Zahlbr.) Wetm., comb. nov.**

*Heppia hassei* Zahlbr., Beih. Bot. Centrbl. 13: 157. 1902. TYPE: California. Palm Springs, ad saxa granitica, *Hasse FN 817*. (Lectotype W.) *Hasse FN 827*. (Syntype FH, NY).

*Heppia murorum* Wain., Acta Soc. Fauna Fl. Fenn. 7(1): 218. 1890 (= Étude Lich. Brésil 1: 218. 1890). TYPE: Brasil. Rio de Janeiro, ad cementum muri, *Wainio, Lich. Brasil. Exs. 190*. (Holotype not seen; isotype FH.)

NOMENCLATORIAL REMARKS. Zahlbruckner cited two collections in the original description of *Heppia hassei*. Only *Hasse Field Number 817* remains in Vienna, and I am selecting this as lectotype. The lectotype packet also contains another species of Heppiaceae with a K<sup>+</sup> red epithecium and loose medulla. I have marked the thallus to be used as the lectotype for var. *hassei*, but the other species needs further study.

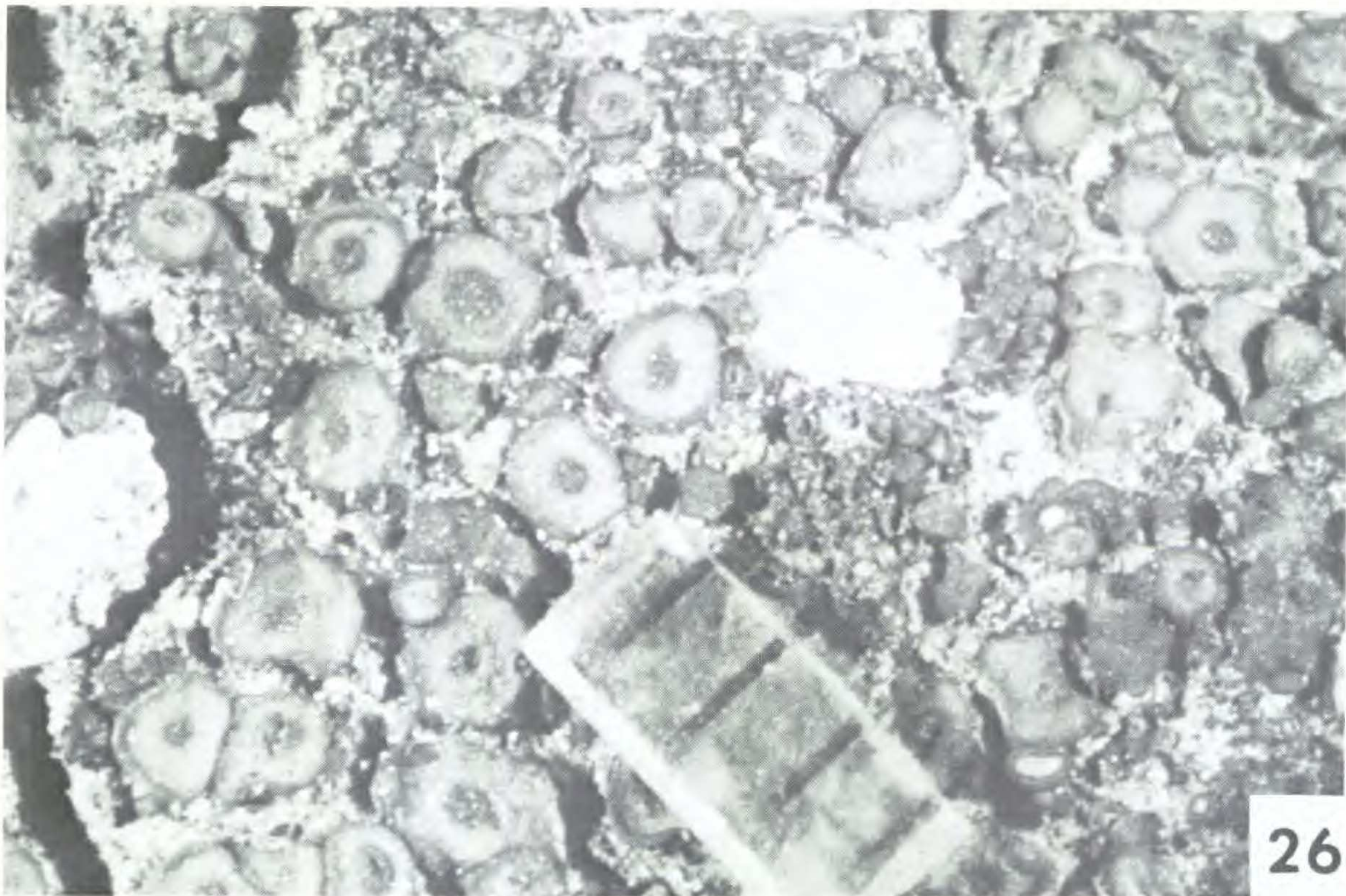
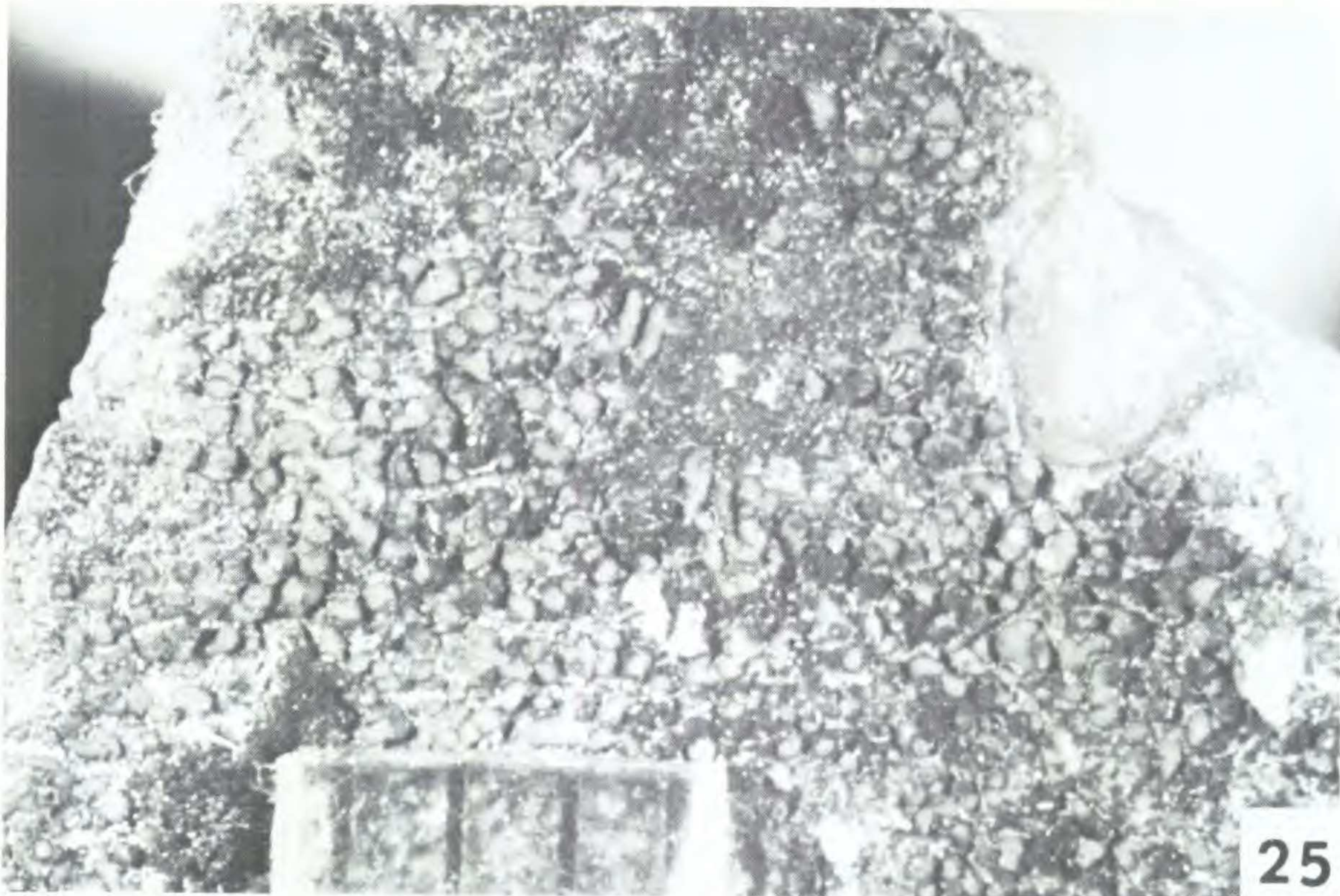
*Heppia murorum* Wain.—See below under taxonomic remarks.

*Thallus* squamulose (Fig. 23), brown to olive-brown; squamules usually deeply lobed and polyphyllous, squamules 1–2 mm diameter, attached by tuft of rhizines or branched umbilicus. Squamules 122–210 $\mu$  thick; upper cortex not developed; lower cortex cellular like medulla but with thicker cell walls, 15–22 $\mu$  thick; medulla cellular but with occasional areas of loose hyphae; algal layer



FIGURES 23-24.—23. *Peltula obscurans* var. *hassei* (Wetmore 16866). Scale divisions are 1 mm each.—24. *Peltula omphaliza* (Wetmore 17045). Scale divisions are 1 mm each.

45–90 $\mu$  thick. Apothecia 1(–3) per squamule, at first immersed but later emergent with thalloid rim; discs 0.5–1.0 mm diameter, sometimes filling whole squamule lobe; epithecium yellow-brown, K<sup>+</sup>; hymenium 120–150 $\mu$  thick; paraphyses 1.5–3.0 $\mu$  thick; asci with gelatinous sheath, 60–68  $\times$  12–18 $\mu$ , containing 100 or more spores; spores oval, 6–7.6  $\times$  3–4.5 $\mu$ . Hymenium I<sup>+</sup> wine-red. Conidia oval to fusiform, 3.1–4.3  $\times$  1.8–2.4 (–3.1) $\mu$  (Fig. 8).



FIGURES 25-26.—25. *Peltula placodizans* (Wetmore 18491). Scale divisions are 1 mm each.—26. *Peltula polyspora* (Wetmore 14707). Scale divisions are 1 mm each.

This variety has an Arid Southwestern distribution (Fig. 35) and in some localities may be fairly abundant. It usually grows on noncalcareous rock but also sometimes on calcareous rock and on soil in rock cracks.

TAXONOMIC REMARKS. Some collections have varying amounts of loose hyphae in the medulla, but this development is always less than in var. *deserticola*.

Sometimes with different sections of the thallus different amounts of cellular development are found. The specimens on hard granite are usually less lobed. See further remarks under the species.

The isotype of *H. murorum* (FH) seems to be this variety, but it is too small to be sure. Lamb (notes in FH) confirms that *Placodium subglebosum* Müll.-Arg. is the same as *H. murorum*, but I have not seen any of the original material of the *Placodium*. If these are identical, the correct epithet for this taxon, when treated as a species, would have to be *subglebosum*. This synonymy is not made here pending study of the holotypes.

The name *Heppia conchiloba* Zahlbr. has been misapplied to this taxon in North America, but the type of *H. conchiloba* is *H. lutosa*.

Exsiccati: *Plitt, Lich. Exs.* 35 (FH), 139 (sub *Heppia polyspora*) (DS, MU), 238 (sub *Heppia conchiloba*) (ABS, F, FH, MU).

ARIZONA. MARICOPA CO.: N of Gila Bend near Buckeye on US 80, *Wetmore 14534A*. Gila Bend, *Hasse*, 1898 (NY). Saucedo Mts., 14 miles S of Gila Bend along Arizona 85, *Wetmore 14539B*, *14543B*. MOHAVE CO.: 27 miles E of Kingman near Hackberry along US 66, *Wetmore 14912*. PIMA CO.: Sierra Tucson, *Pringle*, 1884 (FH, MICH, US). Tumamoc Hill, west outskirts of Tucson, *Weber L-36750* (COLO). Saguaro National Monument NW of Tucson, *Wetmore 14516A*.

CALIFORNIA. COUNTY UNKNOWN: *Hasse* (FH, MICH). KERN CO.: 2.7 miles N of Caliente, *Tavares & Brinson 1156B* (UC). E of Maricopa on California 166, *Wetmore 14799*. LOS ANGELES CO.: Santa Monica Mts., *Hasse* [14 collections made between 1898 and 1911] (ABS, DS, F, FH, MICH, MU, NY, US). Topanga Pass, *Hasse*, 1909 (US), 1908 (FH). San Gabriel Mts., Rubio Canyon, *collector unknown*, 1911 (FH). San Clemente Island, between Eel Point and Seal Cove, west shore of island, *Weber & Santesson L-42663* (COLO). RIVERSIDE CO.: Elsinore, *Hasse*, 1898 (FH, NY, US). S of Cathedral City, *Wetmore 16865*, *16866*, *16869*. San Jacinto Mts., above Palm Desert, *Wetmore 14575*, *14583B*, *14585B*, *14600*, *14601C*. Near western edge of Palm Desert, *Wetmore 16837B*, *16841*, *16842*, *16843*, *16844*, *16852*, *16853*. Palm Springs, *Hasse FN 817* (W), *FN 827* (FH, NY), [7 collections made between 1901 and 1903] (FH, MINN, NY, POM). San Jacinto Mts. at western edge of Palm Springs in Chino Canyon, *Wetmore 14622B*, *14624B*. Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16878*, *16885A*, *16892*, *16899A*, *16900*. Along California 71 a few miles NE of junction with California 79, *Wetmore 16902*, *16919*, *16924*, *16926*. Eden Hot Springs, *Hasse*, 1911 (FH, US). West edge of San Jacinto Mts. above Soboba Hot Springs, NE of Hemet, *Wetmore 14692B*, *14693A*, *14701B*, *14713*, *14721*. S of Riverside near Perris, *Wetmore 14726*. Along US 66 SW of Barstow, 29 miles on Wells-Stoddard Road, *Wetmore 17030*. SAN DIEGO CO.: One mile NW of Descanso, N of US 80, *Wetmore 16962*. SANTA BARBARA CO.: Near Santa Barbara, *Hasse*, 1903 (LAM). SANTA CLARA CO.: Alum Rock Park, *Baltzo*, 1968 (UC). SONOMA CO.: Santa Rosa, *Brown*, 1946 (F). VENTURA CO.: Matilija Canyon, *Hasse*, 1903 (FH). 6.7 miles N of Santa Paula on California 150, *Tavares 1270a* (UC).

NEW MEXICO. COUNTY UNKNOWN: *Greene*, 1880 (US). VALENCIA CO.: Along San Jose River, 3.5 miles SE of Correo on road to Las Lunas, *Shushan & Weber S-6876* (COLO).

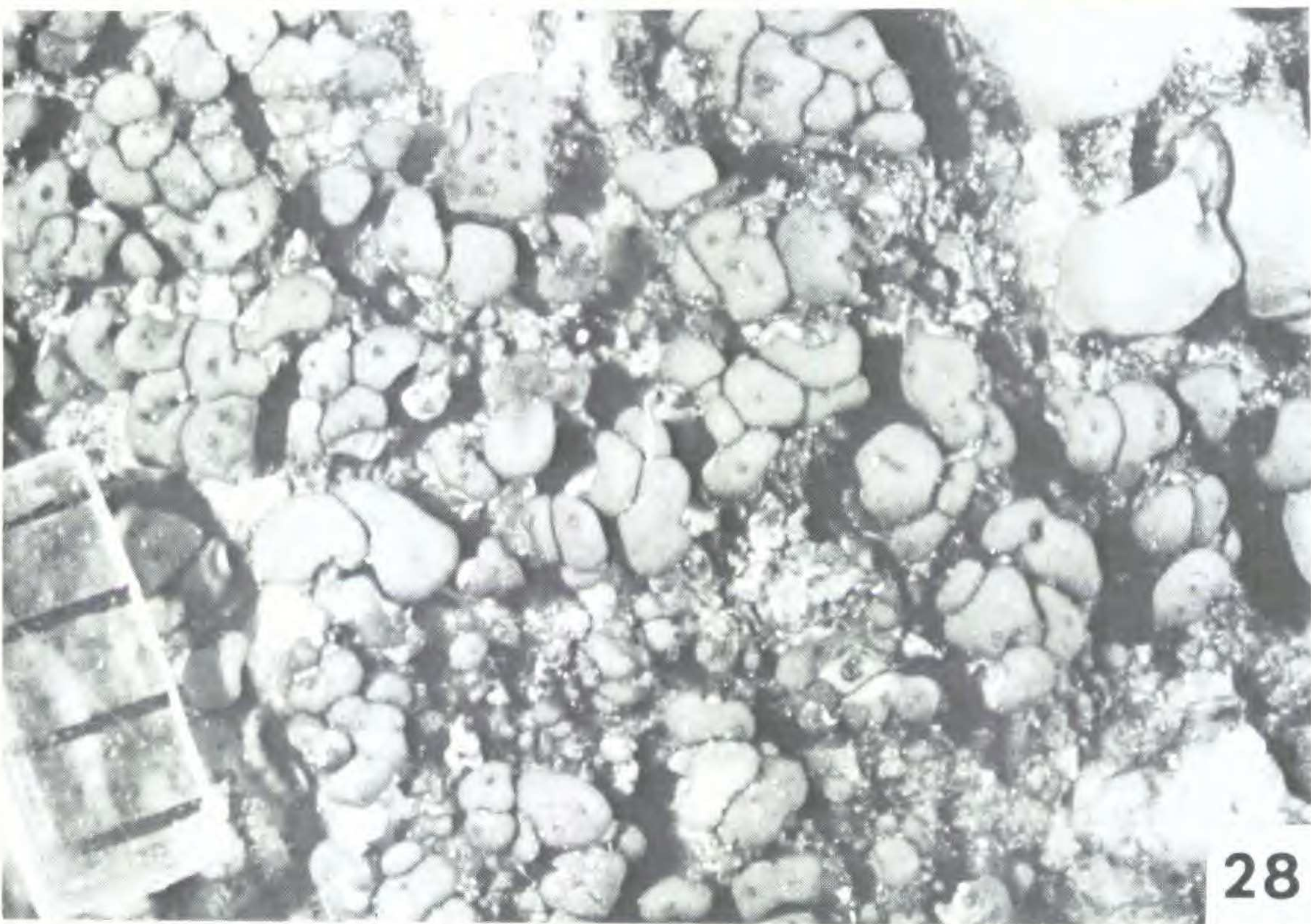
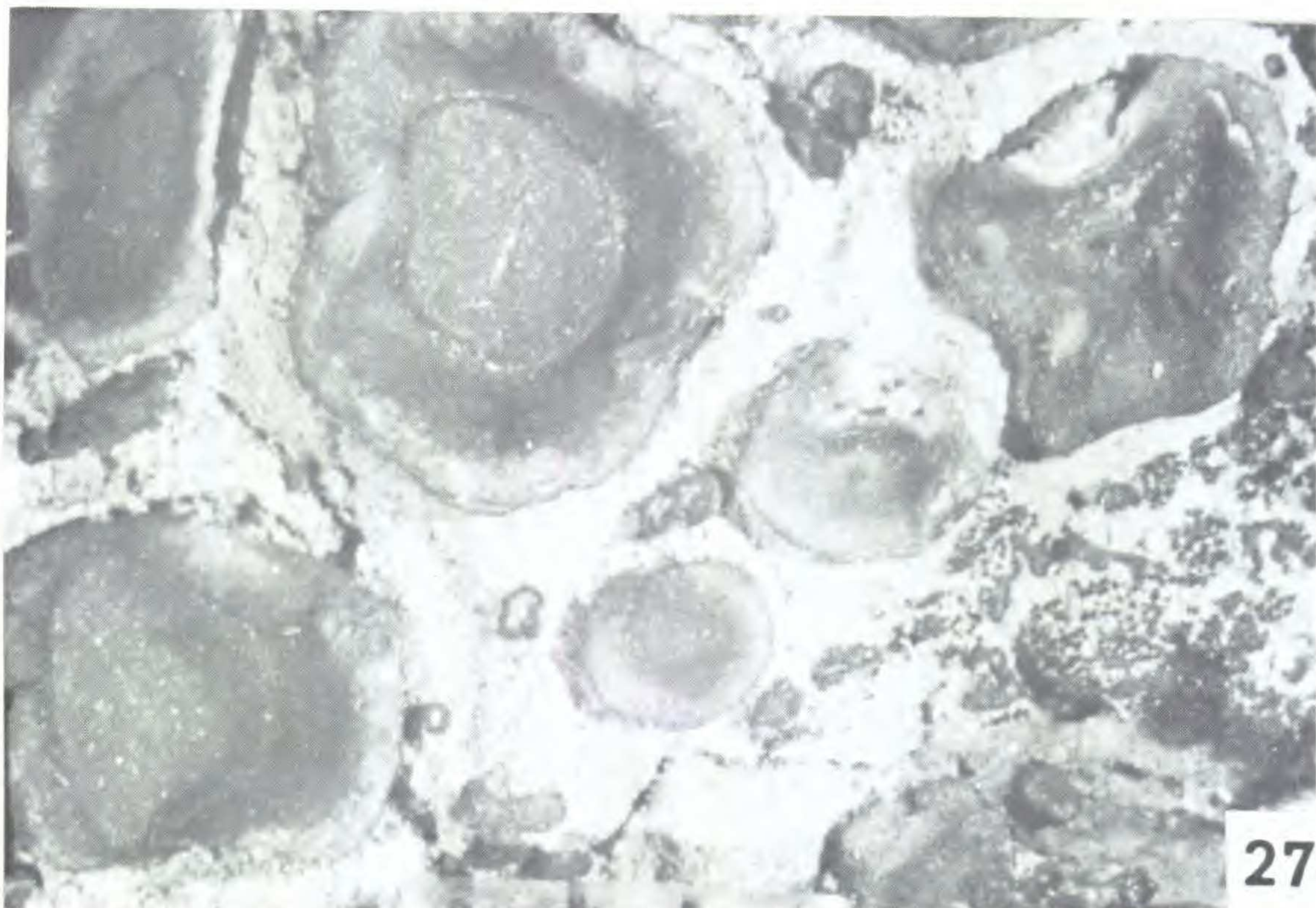
TEXAS. BREWSTER CO.: Big Bend National Park, along Lost Mine Trail from Panther Pass, *Wetmore 14265A*; Pulliam Ridge, *Wetmore 18203B*.

Specimens also seen from Mexico, Brazil, France, and Italy.

***Peltula omphaliza*** (Nyl. in Eckf.) Wetm., comb. nov.

*Heppia omphaliza* Nyl. in Eckf., Bull. Torrey Bot. Cl. 16: 106. 1889. *Endocarpiscum omphalizum* (Nyl. in Eckf.) Müll.-Arg., Hedwigia 34: 28. 1895. TYPE: Mexico. Gulf of California, island of San Pedro Martin, *Palmer*, 1887. (Holotype H-NYLANDER 30893; isotypes F, PH, US.)

NOMENCLATORIAL REMARKS. The holotype is in Nylander's herbarium, but duplicates were found in several other herbaria with varying label data. Some



FIGURES 27-28.—27. *Peltula richardsii* (Wetmore 14541). Scale divisions are 1 mm each.—28. *Peltula zahlbruckneri* (Wetmore 16897A). Scale divisions are 1 mm each.

of the labels even have Eckfelt as the collector. All of the rocks are of the same type and the associated lichens are the same on all pieces. I am confident that the errors in labeling are due to the practices used in distribution of the duplicates.

*Thallus* peltate (Fig. 24), greenish-olive to brownish; squamules 0.5-3 (-4) mm diameter, roundish and convex or slightly lobed and flat; margin finely

wavy; attached by umbilicus. Squamules 153–275 $\mu$  thick; upper cortex not developed; lower cortex of 3–5 layers of cells, 24–36 $\mu$  thick; medulla of loose hyphae; algal layer 90–120 $\mu$  thick. *Apothecia* 5–20 per squamule, totally immersed; disc at first punctiform, later slightly expanded, 0.1–0.2 mm diameter, without thalloid rim; epithecium yellow to yellowish-brown, K<sup>+</sup> red-violet or K<sup>-</sup>; hymenium 120–150 $\mu$  thick; paraphyses 1.5–2.4 $\mu$  thick; asci with gelatinous sheath, 60–75  $\times$  16–23 $\mu$ , containing 100 or more spores; spores ellipsoid to bacilliform 4.6–6.1  $\times$  3.0 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* fusiform, 2.4–3.1  $\times$  1.2 $\mu$ .

*Peltula omphaliza* has an Arid Southwestern distribution (Fig. 36) and will probably be found in many more localities in Mexico. It grows on both calcareous and noncalcareous rock in open exposed areas.

**TAXONOMIC REMARKS.** The epithecium reaction with K is variable even on the same thallus. Probably the reaction is basically K<sup>+</sup>, but sometimes the substance is in low concentration or destroyed by preservation treatments. When the thallus is young it is roundish and convex, but with age and growth it becomes flat and slightly lobed.

ARIZONA. MARICOPA CO.: N of Gila Bend near Buckeye on US 80, *Wetmore 14533B*. Saucedo Mts., 14 miles S of Gila Bend on Ariz. 85, *Wetmore 14543E*. PIMA CO.: Tumamoc Hill, west outskirts of Tucson, *Weber L-36753* (COLO). Saguaro National Monument NW of Tucson, *Wetmore 14514B*, *14515A*.

CALIFORNIA. LOS ANGELES CO.: Santa Monica Mts., *Hasse* (FH). Santa Catalina Island, headland between Cottonwood Canyon and Mills Landing, *Weber & Santesson L-42790* (COLO). RIVERSIDE CO.: Near western edge of Palm Desert, *Wetmore 16850*. Palm Springs, *Hasse FN 901* (FH). Palm Canyon 2.2 miles S of junction with California 111, *Wetmore 16897B*. SAN DIEGO CO.: One mile NW of Descanso north of US 80, *Wetmore 16959A*, *16968*.

NEVADA. CLARK CO: Along US 91 NE of Las Vegas, 22 miles on road going to Axial, *Wetmore 17044A*, *17045*. On road to Mormon Mesa, 14 miles W of Mesquite, *Tavares 1516b*, *1516c* (both UC).

TEXAS. BREWSTER CO.: Big Bend National Park, below Burro Mesa Pourouff, *Wetmore 18312A*; 4 miles W of junction of main road and road to Basin Campground, *Wetmore 18295C*. CULBERSON CO.: 22 miles S of Van Horn, *Anderson & Shushan Sl-8836* (COLO).

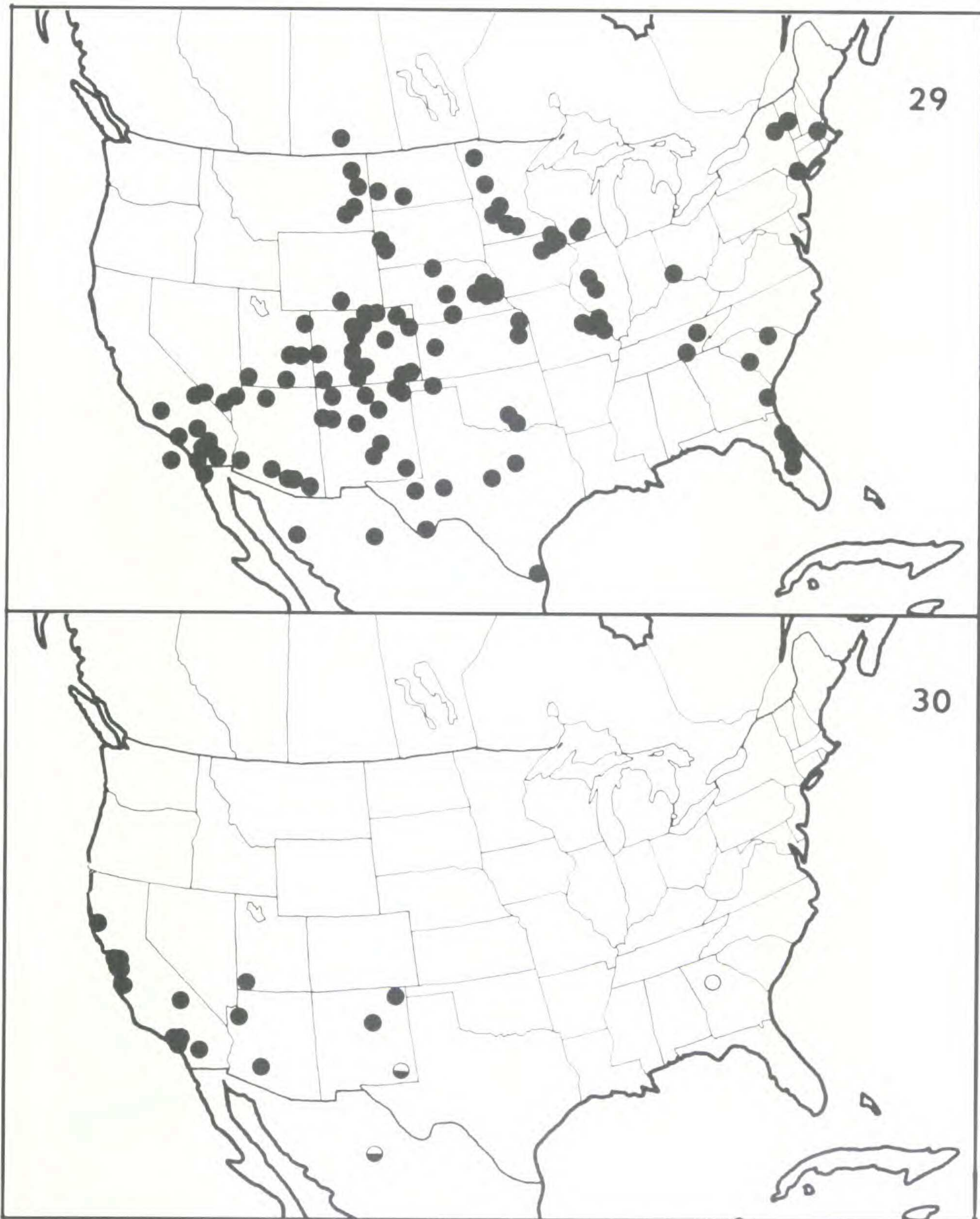
Specimens also seen from Mexico, Equador, France, and Italy.

***Peltula placodizans*** (Zahlbr.) Wetm., comb. nov.

*Heppia placodizans* Zahlbr., Bull. Torrey Bot. Cl. 35: 299. 1908. *Endocarpiscum placodizans* (Zahlbr.) Fink, Mycologia 1: 87. 1909. *Solorinaria placodizans* (Zahlbr.) Gyel., Repert. Spec. Nov. Regni Veg. 38: 307. 1935. *Placoheppia placodizans* (Zahlbr.) Oksn., Fl. Lich. Ucrain. 1: 407. 1956, *comb. inval.* (no basionym cited). TYPE: Arizona. Tucson, Tumamoc Hill, station II, southward facing cliff of boulders, 2600 ft., *Blumer*, 1908. (Holotype W; isotypes DS, FH, MICH.)

**NOMENCLATORIAL REMARKS.** The label data is incomplete on several of the isotype collections and the holotype, but the collection in DS has complete data and the rock chip fits perfectly onto the rock in Vienna!

*Thallus* areolate-placodiform (Fig. 25), brownish to olive-green, 2–8 mm diameter, lobate at margins, areolate in center; lobes 0.2–0.5 mm wide, to 1.3



FIGURES 29–30. The distribution of North American Heppiaceae.—29. *Heppia lutosa*.—30. *Peltula bolanderi*, closed circle; *P. clavata*, half-closed circle; *P. cylindrica*, open circle.

mm long, branched, flat to convex, not inflated; central areoles roundish; whole thallus adnate to substrate, no rhizines or umbilicus apparent; areoles with capitate soralia on upper surface; soredia black, farinose. Thallus 150–244 $\mu$  thick; upper cortex not developed; lower cortex like medulla; medulla cellular;



algal layer 75–90 $\mu$  thick. *Apothecia* one per areole, immersed; disc at first punctiform later to 0.3 mm diameter, without thalloid rim; epithecium yellowish-brown, K<sup>+</sup> or K<sup>-</sup>; hymenium 90–120 (–165) $\mu$  thick; paraphyses 1.5–3.0 $\mu$  thick; asci with gelatinous sheath, containing 100 or more spores; spores globose to subglobose or subfusiform, 3.0–4.6 or 4.5–7.6  $\times$  3.0–4.5 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* oval-fusiform, 3.1–3.7  $\times$  1.8 $\mu$ .

This species has been rarely collected in the southwestern United States, but it probably has a restricted Arid Southwestern distribution (Fig. 37) and will be found to be more abundant in Mexico. It grows on lightly shaded non-calcareous boulders, always in association with *P. euploca*.

**TAXONOMIC REMARKS.** This species probably involves a complex of several lower taxa. However, much more material must be collected over more of its range to be able to divide the group. This is probably a sorediate species, but soredia are not present on all parts of the thallus and sometimes may be rare or absent in any given collection; if abundant thallus is not collected. After close study, the holotype was found to be sorediate. Mexican material often has flat lobes. The epithecial reaction, spores and lobe shape do not appear to correlate yet with other characters to be able to divide the collections into discernable groups.

ARIZONA. COCHISE CO.: Chiricahua Mts., on trail to Silver Peak and Headquarters Gulch, NE of Southwestern Research Station, *Weber, Shushan & Anderson S-24630* (COLO), GRAHAM CO.: Coronado National Forest above Stockton Pass Campground, S of Safford, *Wetmore 14466 p.p.* (sub *P. euploca*). PIMA CO.: Tucson, Tumamoc Hill, *Blumer, 1908* (DS, FH, MICH, W). Tucson Mts., *Darrow 1212* (THOMSON), *Darrow 1214* (COLO, THOMSON).

TEXAS. BREWSTER CO.: Big Bend National Park, across from Basin Campground, *Wetmore 14252A*; Boulder Meadows, *Wetmore 18491*; Grapevine Hills, NW of headquarters, *Wetmore 18293B*; Green Gulch, *Wetmore 18436, 18437A*.

Specimens also seen from Mexico.

***Peltula polyspora*** (Tuck.) Wetm., comb. nov.

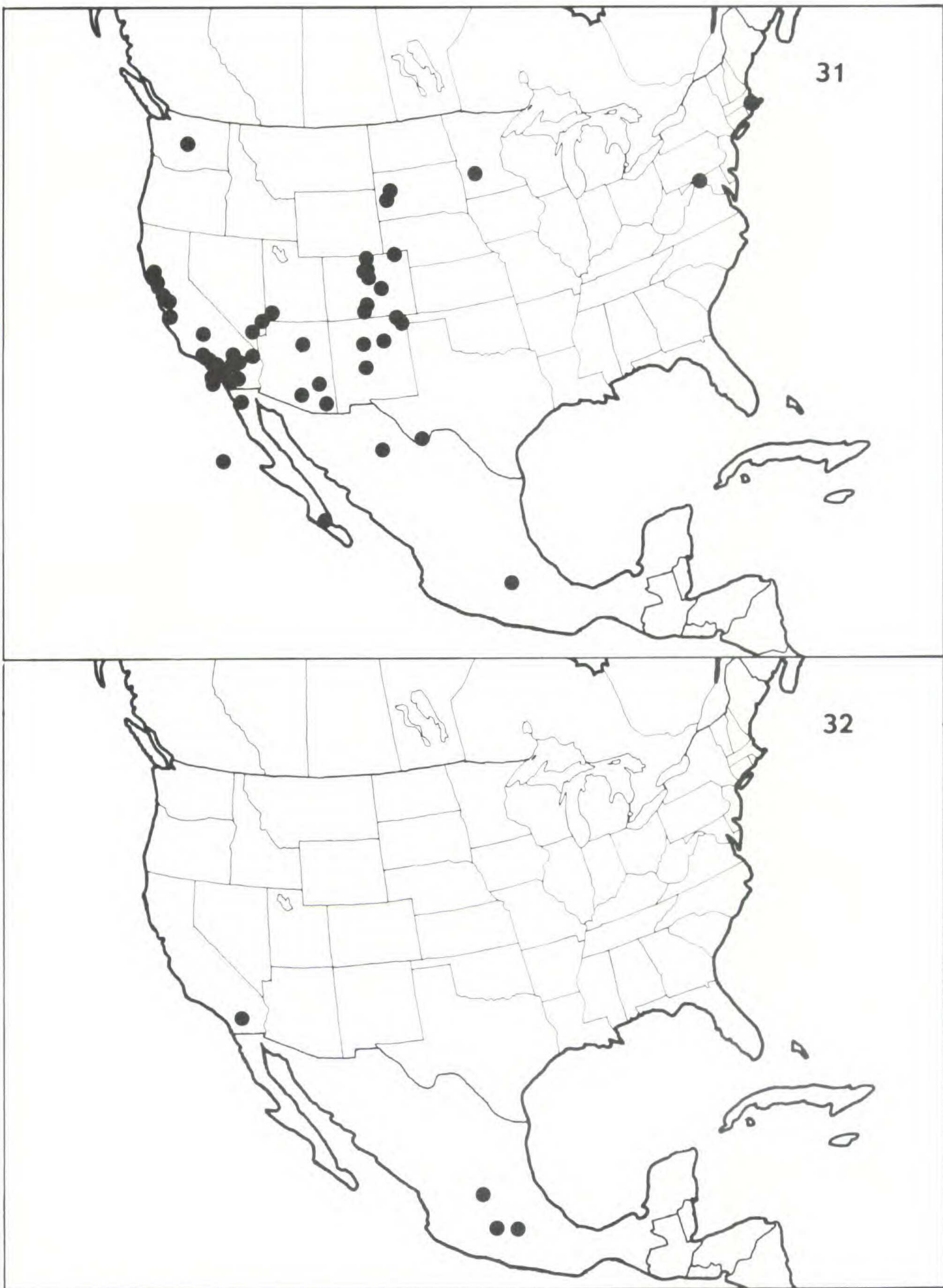
*Heppia polyspora* Tuck., Syn. N. Amer. Lich. 1: 115. 1882. *Endocarpiscum polysporum* (Tuck.) Fink, Contr. U. S. Natl. Herb. 14: 149. 1910. *Heppia arenivaga* Nyl., Lich. Jap. 104. 1890. TYPE: Colorado. *Brandegge*, 1879. (Holotype FH-TUCKERMAN; isotype US.)

*Heppia terrena* Nyl. ex Hasse, Bull. Torrey Bot. Cl. 24: 445. 1897. TYPE: California. Foothills of San Gabriel Mts., new Mt. Wilson's trail, 2500 ft., *Hasse FN 472*, 1896. (Lectotype NY; isolectotypes H-NYLANDER 30950, NY.)

*Heppia leptopholis* Nyl. ex Hasse, Lich. S. Calif. 10. 1898. TYPE: California. Santa Monica Foothills, on clay near Soldier's Home, *Hasse FN 526*. (Lectotype NY; isolectotypes H-NYLANDER 30944, N.Y.)

*Heppia brouardii* B. de Lesd., Bull. Soc. Bot. France 56: 475. 1909. TYPE: Mexico. "Peubla, Cerro Chiquihite, alt. 2205 m., sur la terre, *Frère Arsène Brouard*, 1906." No type material seen.)

**NOMENCLATORIAL REMARKS.** Since no type was designated for *Heppia terrena*, I am selecting *Hasse Field Number 472* in NY as lectotype. The specimen in Nylander's herbarium was not selected because the original description was apparently not written by Nylander but by Hasse. The label data on some of the isotypes is incomplete.



FIGURES 31-32. The distribution of North American Heppiaceae.—31. *Peltula euploca*.—32. *P. michoacanensis*.

*Heppia arenivaga* Nyl was proposed as a *nomen novum* but was unnecessary because no homonyms have been created.

I am selecting the specimen in NY as the lectotype of *Heppia leptopholis* for the same reason as in *H. terrena*. The label data varies on this collection—some with the same field number have the date 1896 and others 1897. These seem to be due to errors in copying labels. Some labels lack locality data.

No type material of *Heppia brouardii* was seen, and none may now exist. One collection identified as this species (Arsène 9633, US) agrees with the original description and was used in interpreting this species.

*Thallus* squamulose (Fig. 26), tan-olive, squamules 1–4 mm diameter, round to sometimes slightly lobed, flat; margins usually thickened and upturned; attached by tuft of hyphae in center. Squamules 183–336 $\mu$  thick; upper cortex not developed; lower cortex of 2–3 layers of roundish cells, 30–40 $\mu$  thick; medulla cellular; algal layer 61–122 $\mu$  thick. *Apothecia* 1–20 per squamule, immersed; disc 0.2–1 mm diameter, occasionally with small thalloid rim; epithecium yellowish-brown, K<sup>+</sup> red-violet; hymenium 120–225 $\mu$  thick; paraphyses 1.5–3.0 $\mu$  thick; asci with gelatinous sheath (Fig. 7), 143–151  $\times$  25–30 $\mu$ , containing 100 or more spores; spores globose, 5.1–5.8 (–8.3) $\mu$ . *Hymenium* I<sup>+</sup> green becoming wine-red. *Conidia* fusiform, 3.7–4.3  $\times$  1.2–2.8 $\mu$ .

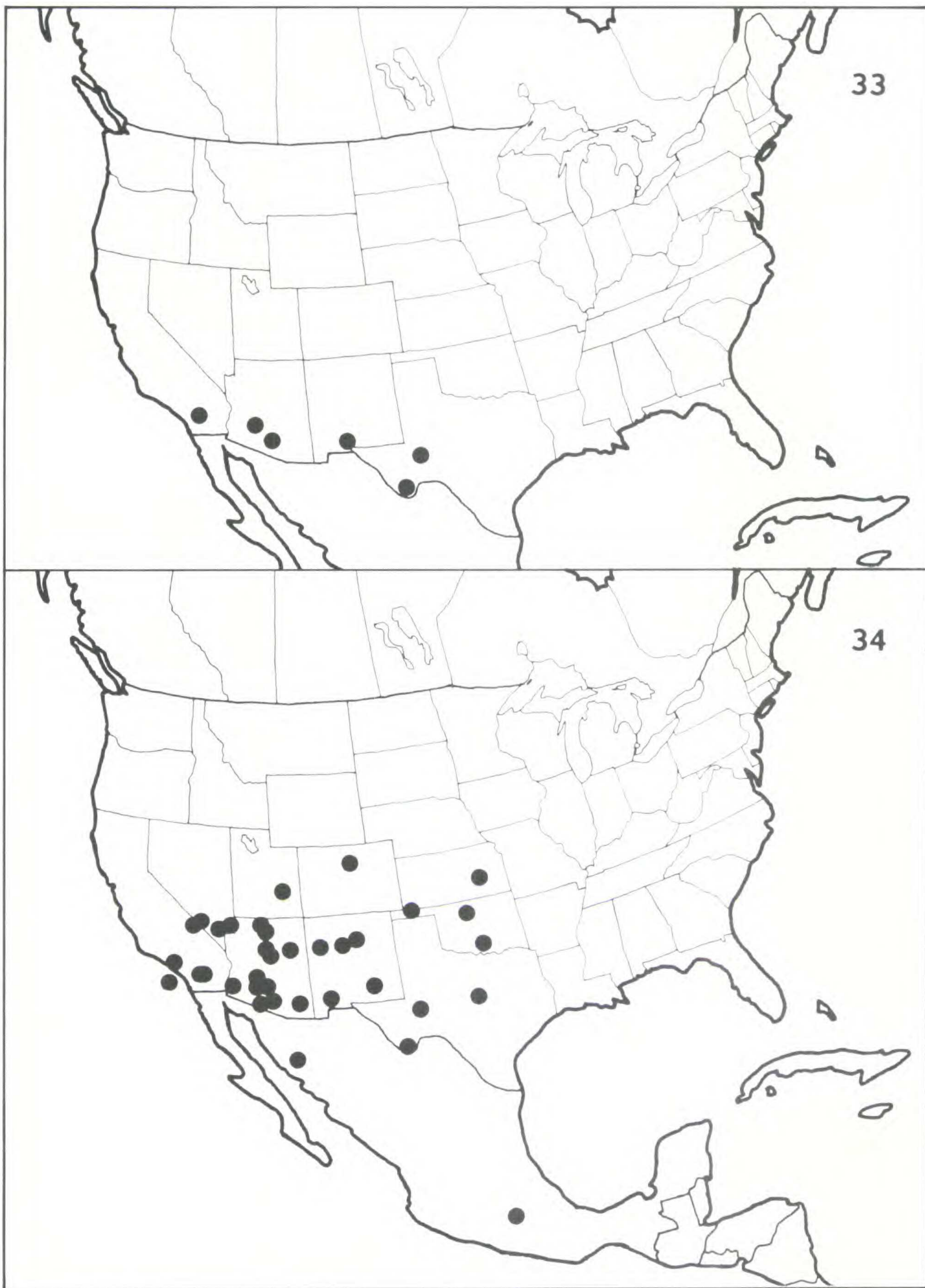
The distribution of *P. polyspora* in North America is somewhat uncertain, but it is probably basically an Arid Southwestern pattern (Fig. 38). The southern Rocky Mountain area needs further study. I found no *P. polyspora* when collecting in this area, but a few isolated plants may be found. This species grows in open dry areas on soil which is usually calcareous.

**TAXONOMIC REMARKS.** Collections with few apothecia have been called *Heppia terrena* and *H. leptopholis*, and those with many apothecia *H. polyspora*. But the production of apothecia is quite variable and does not correlate with any other character and is not worthy of taxonomic recognition.

**Exsiccati:** Hasse, *Lich. S. Calif.* 680 (sub. *Heppia terrena*) (MINN, POM); 891 (sub *Heppia leptopholis*) (LAM, MINN, POM, WIS). Plitt, *Lich. Exs.* 9 (sub *Heppia leptopholis*) (ABS, DS, FH, MU); 34 (sub *Heppia despreauxii*) (ABS); 239 (sub *Heppia terrena*) (DS, FH).

**ARIZONA. COUNTY UNKNOWN:** Pringle 14 (FH, US). Santa Rita Mts., Pringle 4 (COLO, FH, NY). **MARICOPA CO.:** Saucedo Mts., 14 miles S of Gila Bend along Arizona 85, Wetmore 14543A. **PIMA CO.:** Contano, Darrow 527 (LAM). Organ Pipe Cactus National Monument below headquarters, Sierk 2287 (SIERK). Tucson Mt. Park, Imshaug 12890 (MSC). Ledges near Picture Rocks, 12 miles W of Tucson, Bartram 736 (FH). Saguaro National Monument NW of Tucson, Wetmore 14516C. **PINAL CO.:** Picacho Pass NW of Tucson along Interstate 10, Wetmore 14524, 14529B. **YUMA CO.:** Near Mohawk, E of Yuma on US 80, Wetmore 14544A, 14548B.

**CALIFORNIA. COUNTY UNKNOWN:** Hall (MICH). **KERN CO.:** E of Maricopa on California 166, Wetmore 14801, 14807. **LOS ANGELES CO.:** San Gabriel Region, new Mt. Wilson trail, Hasse FN 472 (H, NY). San Gabriel Range, Hasse [6 specimens collected between 1896 and 1904] (FH, MICH, MINN, NY, POM, US). San Gabriel Canyon, Hasse, 1892 (NY). Santa Monica Mts., Hasse [19 specimens collected between 1896 and 1908] (ABS, DS, FH, LAM, H, MICH, MINN, MU, POM, US, WIS); near Soldier's Home, Hasse FN 526 (H, NY), 1897 (FH, MICH, NY, US). Verdigo Mts., Hasse, 1906 (FH). **RIVERSIDE CO.:** Cathedral City, Rose 45338 (COLO); S of Cathedral City, Wetmore 16862, 16867, 16871, 16875. Near western edge of Palm Desert, Wetmore 16834, 16835, 16849, 16854. San Jacinto Mts., above Palm Desert, Wetmore 14583A, 14601B. Palm Springs,



FIGURES 33-34. The distribution of North American Heppiaceae.—33. *Peltula obscurans* var. *obscurans*.—34. *P. obscurans* var. *deserticola*.

*Hasse* "with FN 829" (FH), 1901 (NY), 1903 (FH, NY). San Jacinto Mts. at west edge of Palm Springs in Chino Canyon, *Wetmore* 14612, 14621, 14622A, 14624A. Palm Canyon 2.2 miles S of junction with California 111, *Wetmore* 16876, 16893, 16898. Eden Hot Springs, *Hasse*, 1911 (ABS). San Jacinto Mts. above Soboba Hot Springs (NE of Hemet), *Wetmore* 14690, 14691, 14692A, 14693B, 14694, 14707, 14710, 14720. SAN BERNARDINO CO.: E of South Pass, 12 miles W of Needles, *Drouet & McBride* 4600 (F).

COLORADO. COUNTY UNKNOWN: *Brandegee*, 1879 (FH, US).

MINNESOTA. KANDIYOHI CO.: Locality unknown, *Looman*, 1961 (WIS). YELLOW MEDICINE CO.: Granite Falls, *Fink* 498 (ABS, FH, MICH, MINN, MU, NY, US).

MONTANA. ROOSEVELT CO.: Locality unknown, *Looman*, 1961 (CANL, WIS).

NEBRASKA. CHERRY CO.: Valentine, in city park, *Wetmore* 13098.

NEVADA. NYE CO.: 41 miles ESE of Beaty, *Shushan* Sl-4832 (COLO). CLARK CO.: Devils Canyon, S of Bunkerville on road to Lake Mead, *Tavares* 1766 (UC). Along US 91 NE of Las Vegas 22 miles, on road to Axial, *Wetmore* 17034, 17036, 17040, 17041.

SOUTH DAKOTA. CUSTER CO.: Schenk Canyon (18 miles WSW of Custer), *Wetmore* 11822 (MSC). GRANT CO.: Big Stone, *Williams*, 1894 (FH). PENNINGTON CO.: E of Hayward, 15 miles SW of Rapid City, *Wetmore* 11046 (MSC, WETMORE).

TEXAS. BREWSTER CO.: Big Bend National Park, Green Gulch, *Wetmore* 18443; Old Mine Road near Rio Grande Village, *Wetmore* 18378. JOHNSON CO.: Cleburne State Park (SW of Cleburne), *Wetmore* 14157.

SASKATCHEWAN. ASSINIBOIA CO.: Locality unknown, *Looman*, 1961 (CANL). MIDALE CO.: Locality unknown, *Looman*, 1961 (WIS).

Specimens also seen from Mexico, Cuba, Canary Islands, and Italy.

***Peltula richardsii*** (Herre) Wetm., comb. nov.

*Heppia richardsii* Herre, *Bryologist* 53: 297, 1950. TYPE: New Mexico. Sierra Co., Hot Springs, on dry sandy soil in crevices of rocks, 4000 ft., *Richards & Drouet* 531, 1939. (Holotype LAM; isotype F.)

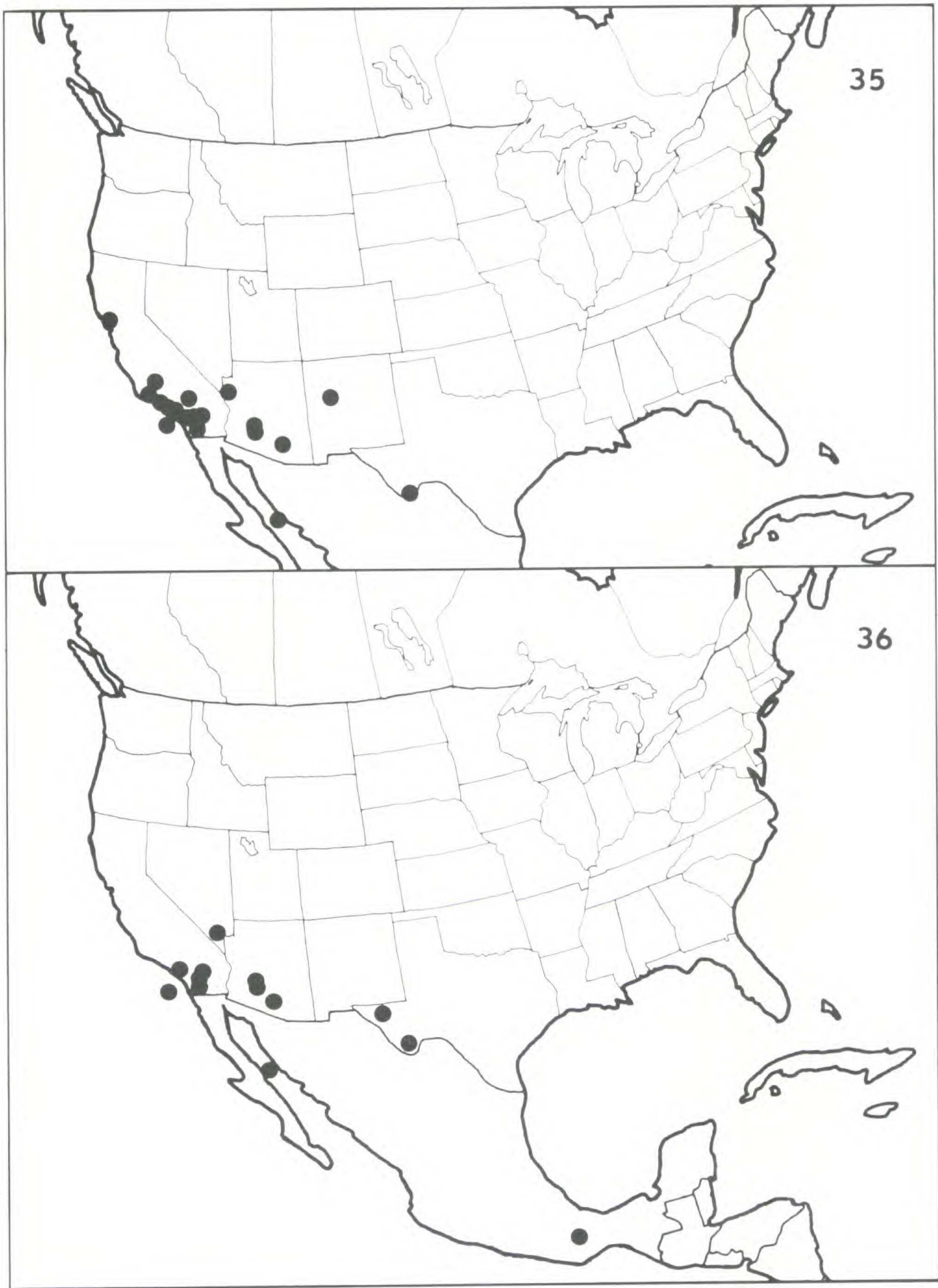
*Thallus* squamulose (Fig. 27), brown-olive; squamules 2–6(–10) mm diameter, round, concave or rarely convex; upper surface smooth and shiny; margin only slightly indented, downrolled; attached by tuft of large rhizines in center. Squamules 250–367 $\mu$  thick; upper surface with amorphous layer over dead algal cells and cellular hyphae, 30–45 $\mu$  thick; lower cortex not developed; medulla of loose hyphae; algal layer 75–105 $\mu$  thick. *Apothecia* one per squamule (rarely 2–3), immersed; disc expanded, 0.5–3(–5) mm diameter, without thalloid rim; epithecium yellow-brown, K<sup>+</sup> red-violet; hymenium 165–170 $\mu$  thick; paraphyses 1.5–3 $\mu$  thick; asci with gelatinous sheath, 140–148  $\times$  30–38 $\mu$ , containing 100 or more spores; spores globose, 6.6–8.3 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* 3.1–3.7  $\times$  1.2 $\mu$ .

Prior to this study this species had been rarely collected, but in some areas I found it to be very abundant. It has an Arid Southwestern distribution (Fig. 39) and grows on soil, which is usually calcareous, in very dry habitats.

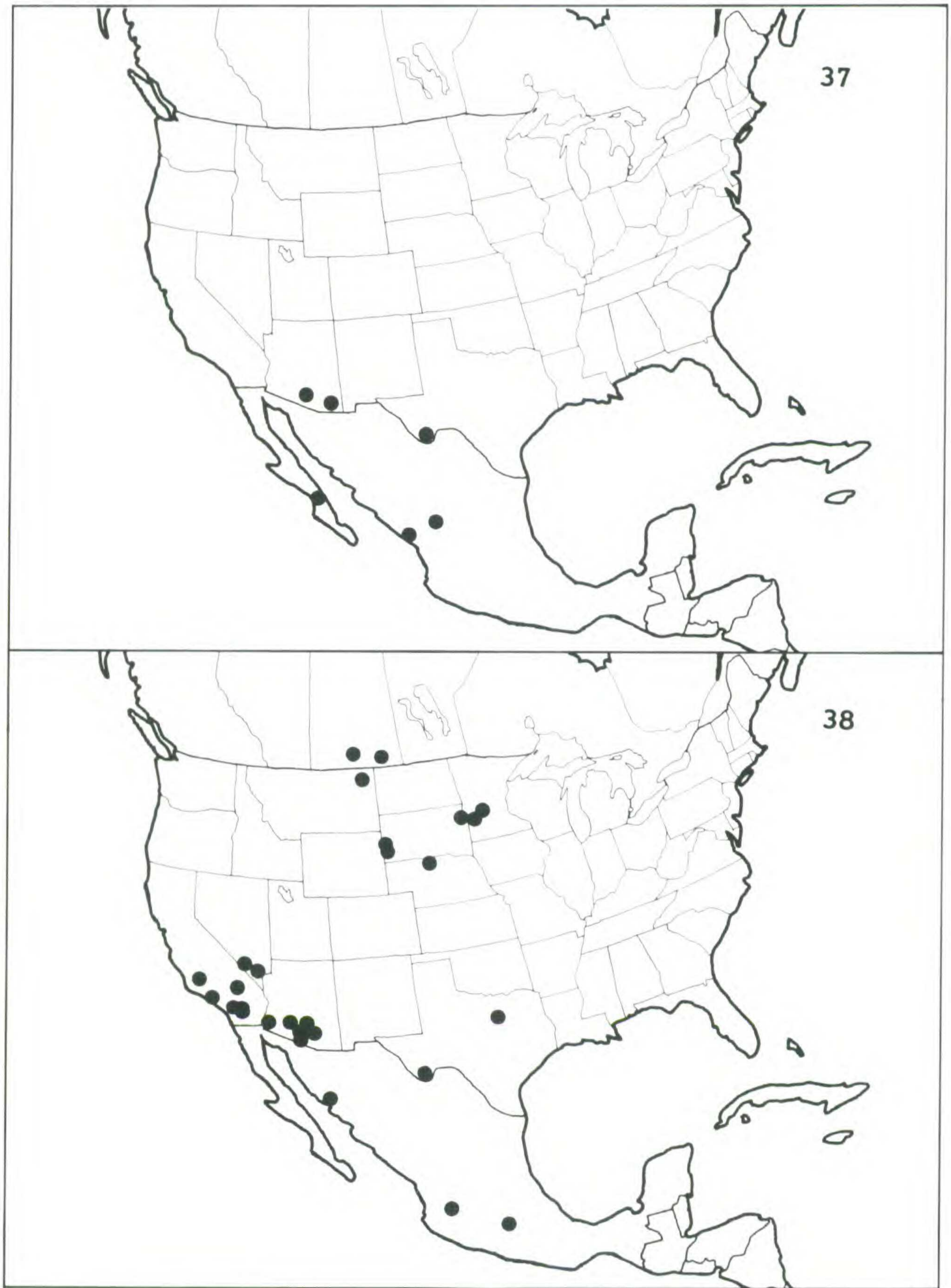
TAXONOMIC REMARKS. The large, shiny squamules with large apothecia easily separate this species from all others.

ARIZONA. MARICOPA CO.: Granite Reef, Forest Camp, *Sierk* 2295 (SIERK). N of Gila Bend near Buckeye on US 80, *Wetmore* 14536. Saucedo Mts., 14 miles S of Gila Bend, *Wetmore* 14541. PIMA CO.: Tucson, collector unknown [probably Blumer], 1908 (DS). PINAL CO.: Picacho Pass NW of Tucson along Interstate 10, *Wetmore* 14529A. YUMA CO.: Near Mohawk, E of Yuma on US 80, *Wetmore* 14545.

CALIFORNIA. RIVERSIDE CO.: San Jacinto Mts. at west edge of Palm Springs in Chino Canyon, *Wetmore* 14615. Near western edge of Palm Desert, *Wetmore* 16846, 16858. S of



FIGURES 35-36. The distribution of North American Heppiaceae.—35. *Peltula obscurans* var. *hassei*.—36. *P. omphaliza*.



FIGURES 37-38. The distribution of North American Heppiaceae.—37. *Peltula placodizans*.—38. *P. polyspora*.

Cathedral City, *Wetmore 16860*.

NEW MEXICO. SIERRA CO.: Hot Springs, *Richards & Drouet, 1939* (F, LAM).

NEVADA. LINCOLN CO.: E of Meadow River between Rox and Carp, *Tavares 1261* (UC).

TEXAS. BREWSTER CO.: Big Bend National Park, W of junction going to Santa Elena Canyon along Texas 170, *Wetmore 14305*; 2 miles W of junction with road to Castolon, *Wetmore 18298*; Hot Springs near Rio Grande Village, *Wetmore 18185*; Old Mine Road near Rio Grande Village, *Wetmore 18380*.

Specimens also seen from Mexico.

***Peltula tortuosa*** (Nees) Wetm., comb. nov.

*Dufourea tortuosa* Nees, *Horae Phys. Berol.* 43. *pl.* 5, *f.* 2. 1820. *Heterina tortuosa* (Nees) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 91. 1857. *Heppia tortuosa* (Nees) Wain., *Acta Soc. Fauna Fl. Fenn.* 7(1): 213. 1890 (= *Étud. Lich. Brésil* 1: 213. 1890). TYPE: Venezuela. Orinoco River, *Humboldt*. (Not seen.)

NOMENCLATORIAL REMARKS. Nylander is often cited as the author of this species, but in his 1857 paper there is no description. Nees von Essenbeck indicates that he was describing a new species and did not refer to *Parmelia tortuosa* Ach., which is another species. See also comments by Henssen (1970).

*Thallus* subfruticose, olive-brown to olive-green; lobes flattened, upright, somewhat branched, often twisted and offset, occasionally partly terete, top often slightly flattened, surface smooth; nonsorediate, nonisidiate; attached by umbilicus. *Thallus* lobes 3–7 mm long, 0.1–0.2 mm thick, 0.4–1.0 mm wide; corticate all around, cortex of 3–4 layers of cells, 10–18 $\mu$  thick; medulla of loose hyphae with hollow areas; algal layer all around, 40–80 $\mu$  thick. *Apothecia* produced on the sides or in swollen ends of lobes, several per lobe, totally immersed with punctiform disc or disc slightly enlarging with age; epithecium yellowish-brown, K<sup>-</sup>; hymenium 150–250 $\mu$  thick; paraphyses thin (1.0–1.5 $\mu$ ), branched but capitate; asci with gelatinous sheath, containing 100 or more spores, 18–25  $\times$  83–110 $\mu$ ; spores globose or subglobose, 4.5  $\times$  3.0–4.5 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* fusiform, 3.1–3.7  $\times$  1.2 $\mu$ .

This species has an uncertain distribution type (Fig. 40) in North America, since I have only seen two collections, both sent to me by Aino Henssen, within the area of this study. It probably will be found in more localities in the future. It grows on granitic rocks. Previous records from Chiricahua Mts., Arizona by Weber (1963) are erroneous. The specimens are *P. clavata*. Henssen (1970) includes some specimens of *P. cylindrica* with *P. tortuosa* in her paper.

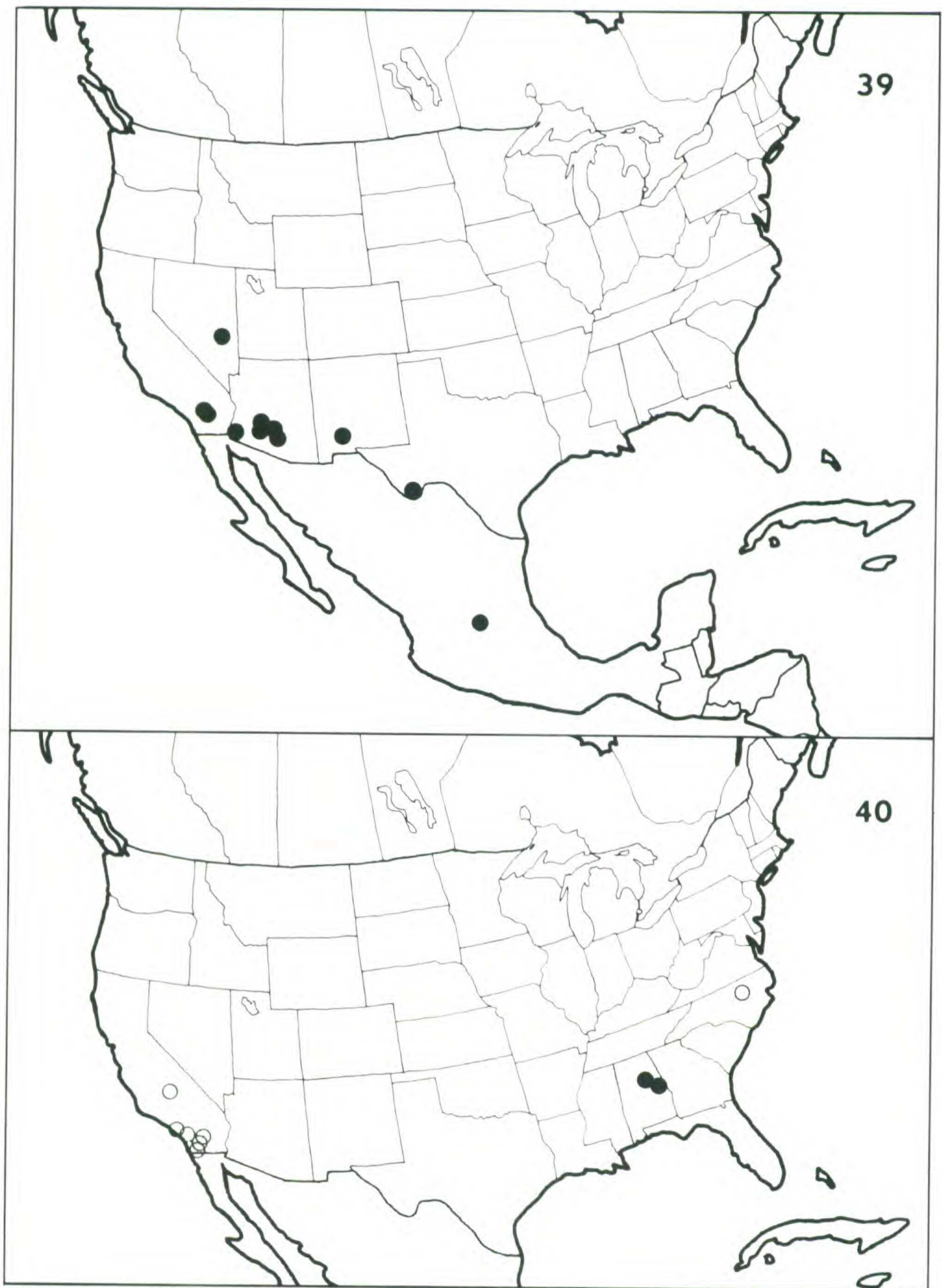
ALABAMA. RANDOLPH CO.: 6 km W of Wadley, E of Ashland, *Henssen 17181B* (HENSSSEN, WETMORE). ST. CLAIR CO.: Cook Springs, 13 km E of Leeds along US 78, *Henssen 15187A* (HENSSSEN, WETMORE).

Specimens also seen from Africa and Venezuela.

***Peltula zahlbruckneri*** (Hasse) Wetm., comb. nov.

*Heppia zahlbruckneri* Hasse, *Bryologist* 14: 100. 1911. TYPE: California. Rubio Canyon, San Gabriel Gelage bei Pasadena, 2500 ft., *Kingman 1159*, 1911. (Holotype W; isotype FH.)





FIGURES 39-40. The distribution of North American Heppiaceae.—39. *Peltula richard-sii*.—40. *P. tortuosa*, closed circle; *P. zahlbruckneri*, open circle.

NOMENCLATORIAL REMARKS. The *Krypt. Vind. Exs.* 1965 indicates that the collection is the "original" collection, however, it also gives Hasse as the collector instead of Kingman so it cannot be the type collection.

*Thallus* areolate-squamulose or sometimes minutely subfruticose (Fig. 28), tan to brownish-olive; squamules swollen, lobed at margins, convex, tops often flattened (especially when young), 0.5–2 mm wide; attached by short stalk and umbilicus. Squamules 153–306 $\mu$  thick; upper cortex not developed; lower cortex with 3–6 layers of roundish cells, 30–56 $\mu$  thick; medulla of loose hyphae with hollow areas; algal layer 75–150 $\mu$  thick. *Apothecia* 1–7 per areole, totally immersed; disc punctiform, without thalloid rim; epithecium brownish, K<sup>-</sup>; hymenium 105–150 $\mu$  thick; paraphyses 1.5–3 $\mu$  thick; asci with gelatinous sheath, 98–113  $\times$  18–23 $\mu$ , containing 32–100 or more spores; spores globose to subglobose, 4.5–7.6  $\times$  3.0–4.5 $\mu$ . *Hymenium* I<sup>+</sup> wine-red. *Conidia* fusiform, 3.0–4.5  $\times$  1.5 $\mu$ .

*P. zahlbruckneri* occurs in southern California and North Carolina according to present information (Fig. 40), but it probably will be found in other places also. It grows on the north sides of large granite rock ledges and covers large areas in some localities (e.g., Palm Springs, California, Fig. 15).

When I visited Rubio Canyon (the type locality) in 1966, no undisturbed rock areas could be found, and a large housing development had been built in the canyon.

TAXONOMIC REMARKS. Young asci have over 100 spores, but as the ascus matures fewer spores are found. In some cases I have seen about 60. Hasse mentioned 24–32 in the original description, but some apothecia of the type have 100 spores. This species never gets tall and cylindrical like *P. cylindricia*, but in some other ways these two species are similar.

Exsiccati: *Krypt. Vind. Exsicc.* 1965 (F, FH, NY, US). *Plitt, Lich. Exs.* 60 (ABS, FH, OS, MU).

CALIFORNIA. LOS ANGELES CO.: San Gabriel Range, Hasse (MICH); Pasadena, Kingman 1159 (FH, W), 1310 (ABS); Rubio Canyon, Hasse, 1911 (ABS, FH), Hasse, 1911 (ABS, LAM), Hasse, 15 April 1911 (FH, US), Hasse (F, FH, NY, US), collector unknown, May 1911 (FH). Santa Monica Range, Hasse, 1913 (ABS, FH, OC, OS); Topanga Canyon, collector unknown, 1901 (FH). RIVERSIDE CO.: Eden Hot Springs, Hasse, 1911 (FH, US). San Jacinto Mts., above Palm Desert, Wetmore 14582, 14591; near western edge of Palm Desert, Wetmore 16857. Palm Springs, Hasse, 1903 (FH, NY, US); west edge of Palm Springs in Chino Canyon, Wetmore 14608. Palm Canyon S of California 111, Wetmore 16881B, 16897A. Near Riverside, Reed 3171 (FH). SAN DIEGO CO.: One mile NW of Descanso, Wetmore 16972. TULARE CO.: 3 miles SE of Exeter at Rocky Hill, Weber L-38587 (COLO). VENTURA CO.: 4 miles N of Newbury Park on Ventura Blvd., Weber S-1748 (COLO).

NORTH CAROLINA. WAKE CO.: 30 km N of Raleigh, south bank of Little River, Henssen 17162B (WETMORE).

#### SPECIES OF DOUBTFUL PLACEMENT AND ERRONEOUS RECORDS

*Heppia alumenensis* Herre, *Bryologist* 15: 84. 1912.—The type collection could not be found in any North American herbarium, nor was it in Vienna. No authentic material has been found, and no material has been seen that has ever been given this name. Collections made at the type locality (Alum Rock Park, California) by Tavares and her students failed to turn up any Heppiaceae that agreed with the original description. The type may have

been destroyed, or it may yet turn up in some herbarium. Placement of this taxon must await finding authentic material.

*Heppia planescens* Nyl., Syn. Lich. 2: 46. 1885.—The type could not be located in Helsinki. It was apparently sent to Hariot in Paris on loan in 1914 and never returned. It may someday be found in Paris. No other authentic material has been seen, and none is in the Tuckerman Herbarium (FH).

*Heppia psammophila* Nyl., Flora 61: 339. 1878.—Hasse (1915) reported this species from Barton's Peak, Santa Monica Range, California, but no specimen from that locality has been seen. No other records of *H. psammophila* were found and the report is probably based on an incorrect identification. I have examined the type in Nylander's herbarium (H), and I have seen no North American material that can be assigned to this species.

## INDEX TO EXSICCATI

In this list only collections from North America are included.

- Hasse, Lich. S. Calif. 680 (sub *Heppia terrena*) = *Peltula polyspora* (MINN, POM).  
 Hasse, Lich. S. Calif. 891 (sub *Heppia leptopholis*) = *Peltula polyspora* (LAM, MINN, POM, WIS).  
 Krypt. Vind. Exs. 1965 (sub *Heppia zahlbruckneri*) = *Peltula zahlbruckneri* (ABS, FH, OS, MU).  
 Plitt, Lich. Exs. 9 (sub *Heppia leptopholis*) = *Peltula polyspora* (ABS, DS, FH, MU).  
 Plitt, Lich. Exs. 34 (sub *Heppia despreauxii*) = *Heppia lutosa* (DS, FH, MU); = *Peltula polyspora* (ABS).  
 Plitt, Lich. Exs. 35 (sub *Heppia hassei*) = *Peltula obscurans* var. *hassei* (FH); = *Peltula obscurans* var. *obscurans* (ABS, FH).  
 Plitt, Lich. Exs. 138 (sub *Heppia bolanderi*) = *Peltula bolanderi* (ABS, FH, MU); = *Peltula obscurans* var. *deserticola* (DS).  
 Plitt, Lich. Exs. 139 (sub *Heppia polyspora*) = *Peltula bolanderi* (ABS, FH); = *Peltula obscurans* var. *hassei* (DS, MU).  
 Plitt, Lich. Exs. 238 (sub *Heppia conchiloba*) = *Peltula obscurans* var. *hassei* (ABS, F, FH, MU).  
 Plitt, Lich. Exs. 239 (sub *Heppia terrena*) = *Peltula polyspora* (DS, FH); = *Heppia lutosa* (ABS, MU).  
 Zahlbr., Lich. Rar. 90 (sub *Heppia bolanderi*) = *Peltula bolanderi* (FH).

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